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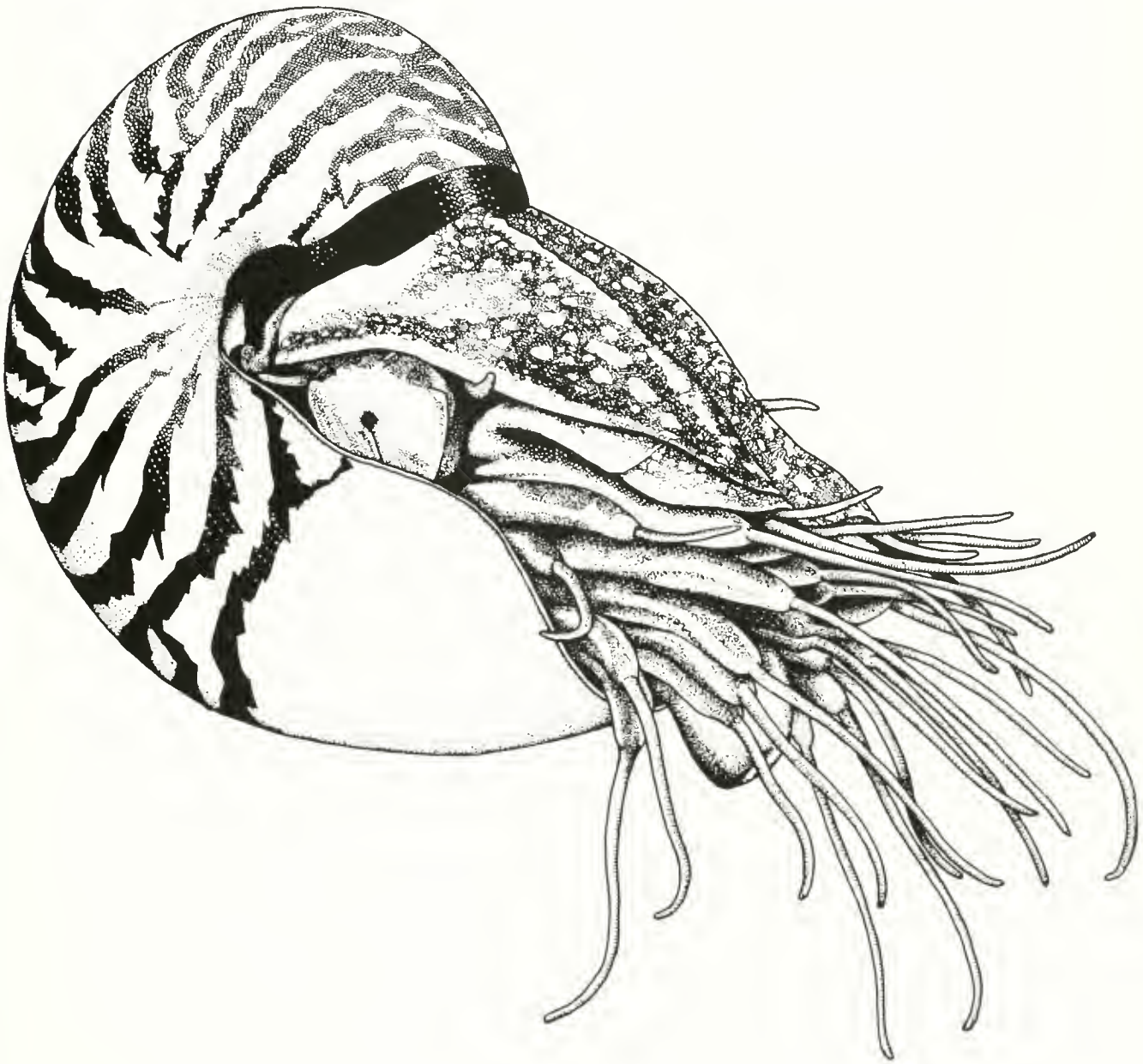

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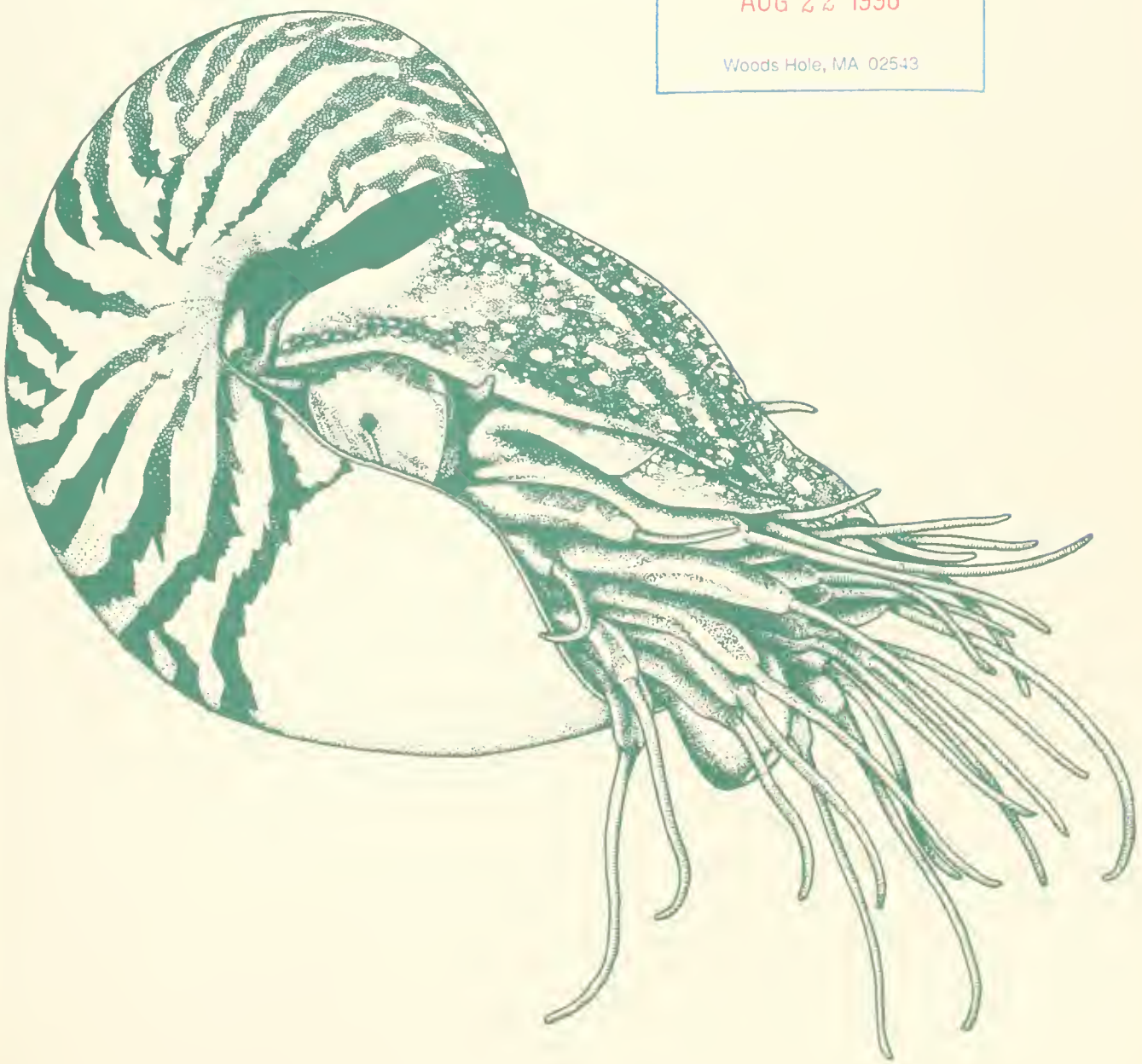

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Time Course of Tissue Specific Metabolism of the Subtidal Gastropod *Hexaplex trunculus* under Anaerobic Conditions

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ABSTRACT

Anaerobic energy metabolism was investigated in foot, mantle and hepatopancreas of the subtidal gastropod *Hexaplex trunculus* (Linné, 1758) (=*Murex trunculus*). Changes in the levels of adenylates, substrates and end products were monitored over a time course of 16 hours of anoxia. It is suggested that unlike intertidal species, the succinate pathway is a metabolic route of minor importance during anoxia in subtidal gastropods. The existence of an alternative electron acceptor, apart from O_2 and fumarate, in the tissues of the subtidal gastropods under anaerobic conditions is discussed.

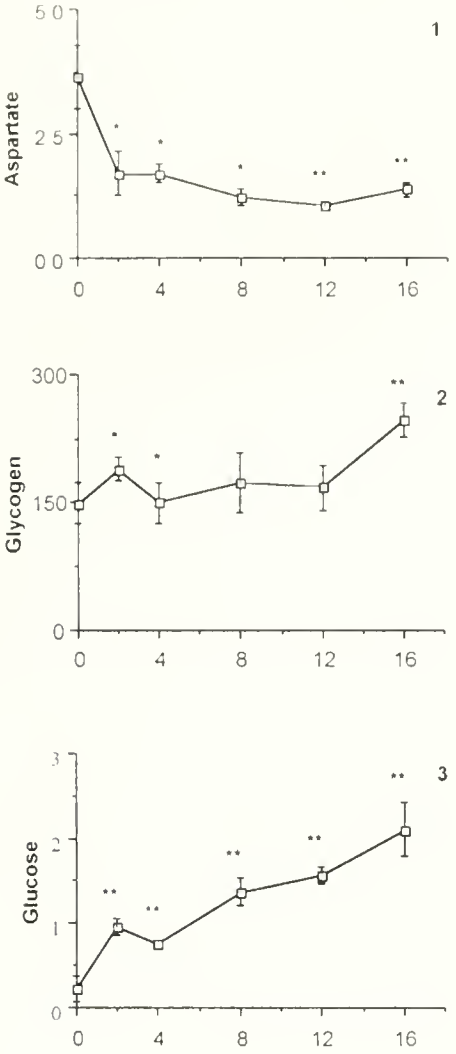
Key Words: metabolism, anaerobiosis, subtidal, gastropods, foot, mantle, hepatopancreas, *Hexaplex trunculus*.

INTRODUCTION

It is generally accepted that within the animal kingdom the ability to sustain periods of oxygen deprivation varies among the different phyla. Mollusks and particularly bivalves present well developed capacities for the survival of environmental anoxia and for this reason have been extensively studied in terms of their anaerobic energy metabolism (de Zwaan, 1983).The available literature on molluscan metabolism during anaerobiosis deals with metabolic responses of separate tissues, as well as with comparative differences and similarities of carbohydrate catabolism of various organs. The data on metabolic tissue specific differences derive mainly from studies on the bivalve *Mytilus edulis* Linné, 1758 (Livingstone & Bayne, 1976; Kluytmans *et al.*, 1977; Zurburg & Kluytmans, 1980), on the cherrystone clam *Mercenaria mercenaria* Linné, 1758 (Korycan & Storey, 1983), on the oyster *Crassostrea virginica* (Gmelin, 1791) (Eberlee *et al.*, 1983), on the common cockle *Cardium edule* Linné, 1758 (= *Cerastoderma edule*)(Meinardus & Gäde, 1981) and on the marine whelk *Busycotypus canaliculatum* (Linné, 1758) (Storey, 1988; Eberlee & Storey, 1988; Whitman & Storey, 1989; Storey *et al.*, 1990), where it is suggested that the metabolic response of different tissues during anaerobiosis and recovery differs quantitatively but not qualitatively. Succinate and alanine were found to be the main end products of anaerobiosis in all tissues studied (Kluytmans *et al.*, 1977; Zurburg & Kluytmans, 1980; Meinardus & Gäde, 1981; Eberlee *et al.*, 1983; Korycan & Storey, 1983; Eberlee & Storey, 1988; Storey *et al.*, 1990), whereas glycogen and aspartate served as the major substrates of anaerobic fermentation (Korycan & Storey, 1983, Eberlee & Storey, 1988).

The above pattern of tissue specific response refers to studies made mainly on species living in the intertidal zone, in which exposure to air is a relatively common occurence. Consequently very little information is available on metabolic tissue specificities of subtidal species (Wieser, 1980; Carpené *et al.*, 1981; Gäde *et al.*, 1984) concerning mainly some end products of their anaerobic metabolism. *Hexaplex trunculus* is reported to be capable of sustaining oxygen depletion for a period up to 100–200 hours (Zs Nagy, 1971). This species normally lives in the subtidal zone, where it may be exposed to anoxic conditions caused by a variety of factors, including for instance severe water pollution combined with high water temperatures. Despite the variety of studies on anaerobic metabolism of intertidal species, no substantial information is available on the potential mechanisms of anoxia tolerance of subtidal species. Therefore, we examined metabolic patterns used under anaerobic conditions in different tissues of *Hexaplex trunculus*. Comparison of the overall anaerobic metabolism of subtidal and intertidal species show substantial tissue specific differences in the time course of metabolic changes during anaerobiosis, as well as in the products accumulated and substrates utilized. In addition, the comparison of the general response between intertidal and subtidal gastropods revealed a different metabolic scheme concern-

* Author to whom correspondence should be addressed.



Figs 1–3. Changes in the concentrations of aspartate, glycogen and glucose in the hepatopancreas of *Hexaplex trunculus* during various periods of anaerobiosis 1) aspartate, 2) glycogen, 3) glucose. * Significantly different from the corresponding aerobic condition (t-test $P<0.05$). ** Significantly different from the corresponding aerobic condition (t-test $P<0.005$)

ing the use of the succinate pathway by *Hexaplex trunculus* tissues during anaerobiosis.

MATERIALS AND METHODS

Animals and Chemicals: Specimens of *Hexaplex trunculus* were obtained from the shores of Thessaloniki through a local fisherman. They were kept in circulating seawater at about 20°C and were used two to three days after arrival. Aerobic animals were sampled directly from the seawater tank. To impose anoxia the animals were placed in a vessel of seawater with an air tight cover, containig 1 L of seawater that had been previously deoxygenated by bubbling a steady stream of nitrogen gas through it for 1 h to give zero oxygen tension as monitored with an oxygen electrode (Digital Oxygen System, model 10, Rank Brothers Manufacture). Animals were kept under anoxic conditions for 2, 4, 8, 12 and 16 h at 20°C. At the end of the anoxic incubation the shells were quickly opened and the tissues were rapidly excised, blotted and immediately frozen in liquid nitrogen. Tissues were stored at -80°C until assayed.

Substrates, enzymes and coenzymes were purchased from Sigma Chemicals Co. (St Louis, USA). All other chemicals were purchased from Serva (Heidelberg, Germany).

Preparations of Tissue Extracts: Samples of frozen tissue were ground to a powder under liquid nitrogen using a mortar and a pestle. The powdered tissue was extracted by adding three volumes of cold perchloric acid ($HClO_4$, 10% w/v). The precipitated protein was removed by centrifugation at 4000 × g for 10 minutes and the supernatants were neutralized with 3M potassium bicarbonate ($KHCO_3$).The precipitated potassium perchlorate was removed by centrifugation as above and the supernatants were taken for determination of metabolite concentrations.

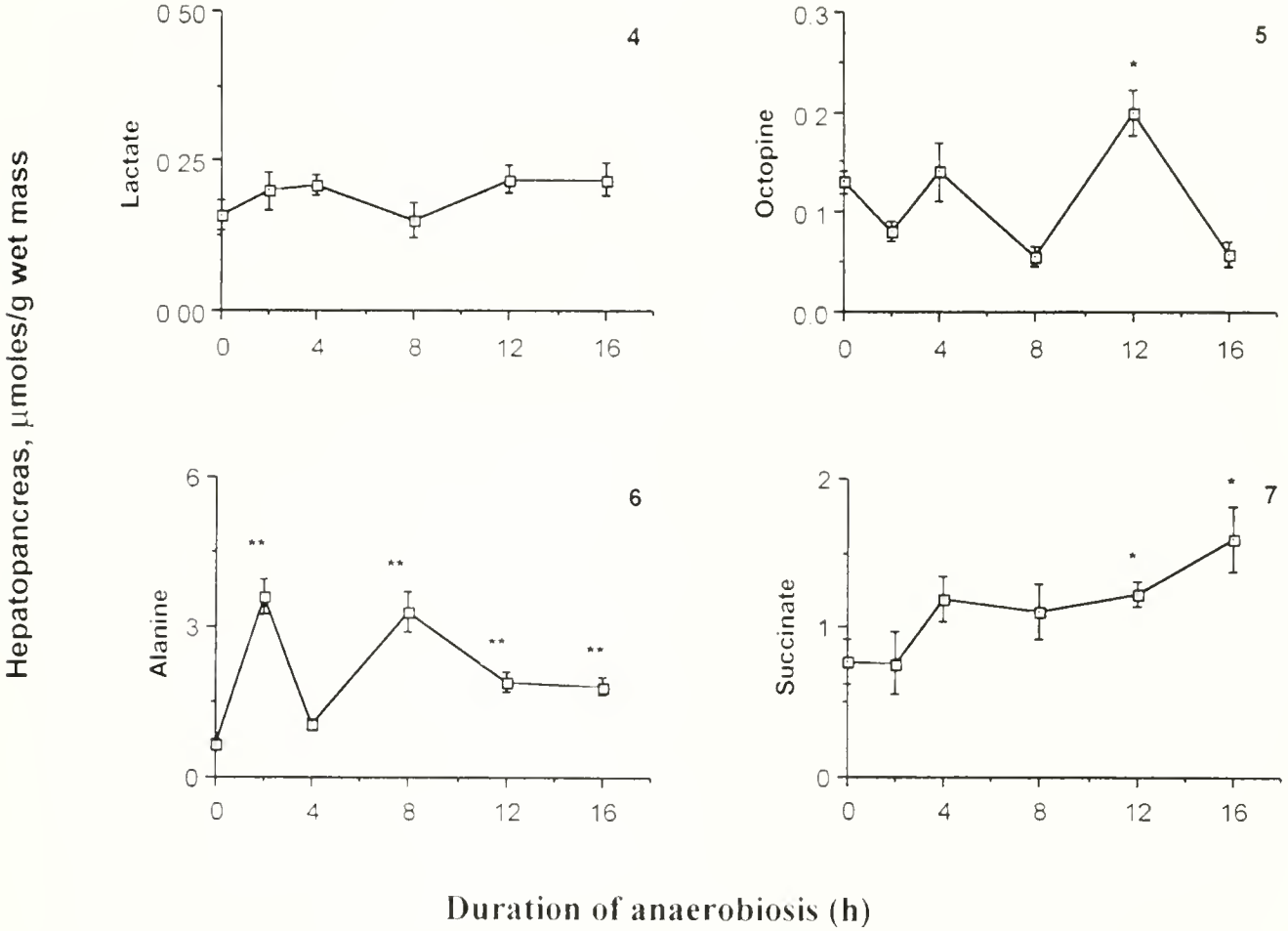
Determination of Metabolites: Glycogen was determined by the method of Keppler and Decker (1974), aspartate by the method of Bergmeyer *et al.* (1974a) and glucose by the method of Bergmeyer *et al.* (1974b). Alanine was assayed according to Williamson D.H.(1974) and succinate according to Williamson J.R. (1974). L-Lactate was measured according to Gutmann and Wahlefeld (1974) and octopine according to Storey *et al.* (1979). ATP was quantified by the method of Lamprecht and Trautschold (1974), ADP and AMP by the method of Jaworek *et al.* (1974).

Statistics: Results are presented as means ± SEM (n=5). Tests for significant differences between groups used the Student's t-test.

RESULTS

Hepatopancreas: Figures 1–3 show the changes in aspartate, glycogen and glucose content of the hepatopancreas of *Hexaplex trunculus* during 16h of anaerobiosis. Aspartate content decreased throughout all the periods of anoxia tested. Aspartate levels measured in the tissue were lowest after 12h of anaerobiosis. Glycogen and glucose levels tended to increase throughout anaerobiosis. Glucose concentration increased 10-fold during 16h of anoxia.

Figures 4–7 illustrate the time course of the changes



Figs 4–7. Changes in the concentrations of lactate, octopine, alanine and succinate in the hepatopancreas of *Hexaplex trunculus* during various periods of anaerobiosis. 4) lactate, 5) octopine, 6) alanine, 7) succinate. * Significantly different from the corresponding aerobic condition (t-test $P<0.05$). ** Significantly different from the corresponding aerobic condition (t-test $P<0.005$)

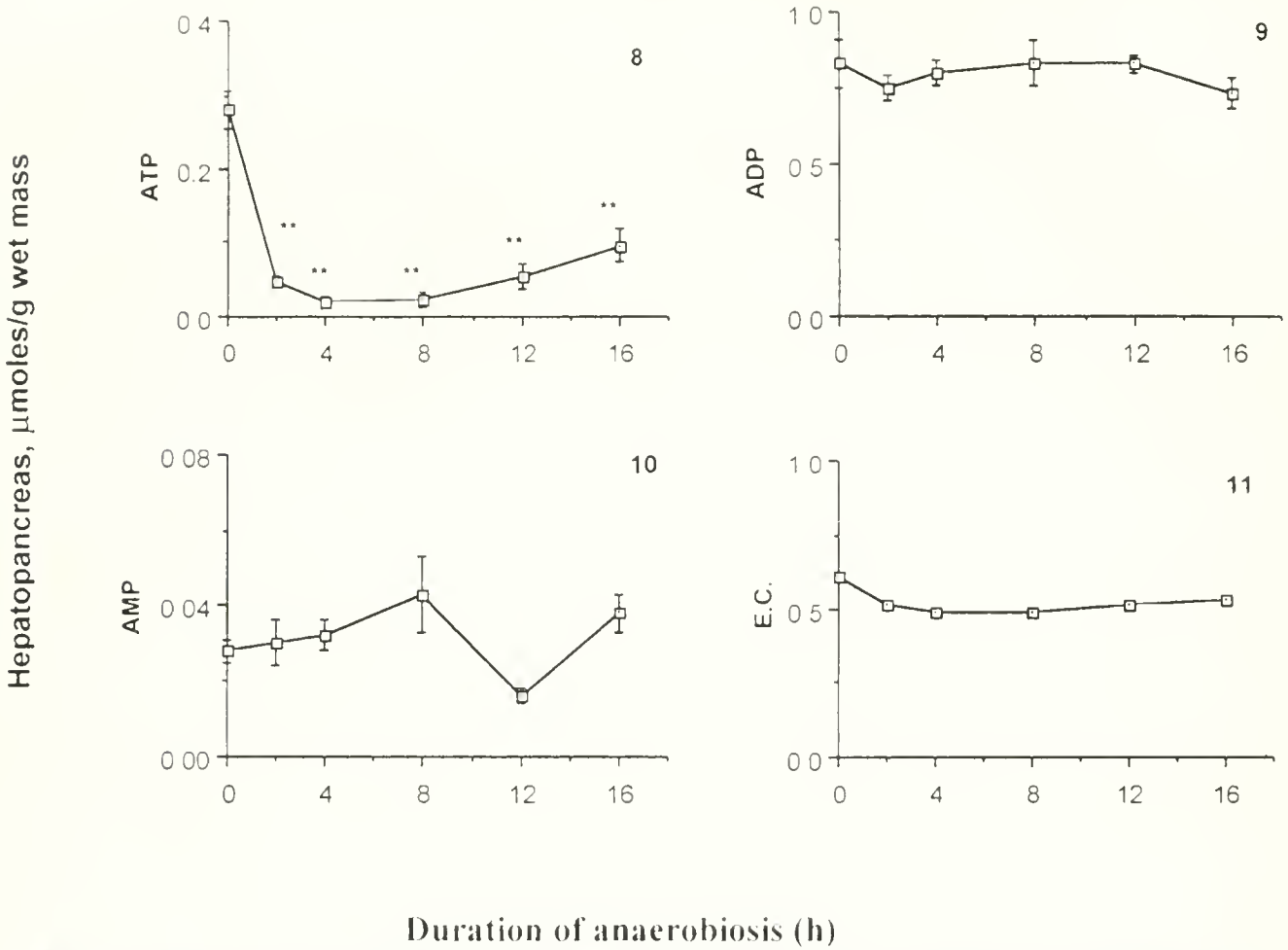
in levels of potential end products of *Hexaplex trunculus* hepatopancreas during anoxia. Alanine accumulated during the first hours of anoxia. Thereafter its levels started to fall, but remained significantly increased compared to the aerobic state. Succinate accumulated after the 4th hour of anoxia. The maximum alanine accumulation (2.9 µmol/g wet mass) observed during the first two hours of anoxia exceeded that of succinate (0.8 µmol/g wet mass) observed after 16 h of anaerobiosis. Octopine accumulated significantly after 12h of anoxia, while no significant lactate accumulation was observed throughout the 16h anaerobiosis.

From the data shown in figures 8–11 a sharp decline in ATP content can be detected, while levels of ADP and AMP are not significantly changed. The energy charge shifts from 0.61 to 0.49 after 4h of anoxia. Thereafter, it slightly increases to 0.53 after 16h of anoxia.

Foot Muscle: Figures 12–14 show changes in concentrations of aspartate, glycogen and glucose in the foot muscle of *Hexaplex trunculus* during 16h of anoxia. As in the hepatopancreas, aspartate levels had fallen significantly by the 4th hour of anoxia. At that time its levels are reduced by 5.5 µmol/g wet mass. Thereafter, its concentration remained almost constant. Contrary to the results in hepatopancreas, glycogen levels had fallen by the 4th hour of anoxia. After 8h of anaerobiosis a sharp reduction in glycogen content was observed (44.2 µmol/g wet mass). Glucose levels were significantly increased after 8 hours, after 12h of anaerobiosis its concentration was almost double that of the aerobic state.

Changes in the concentrations of lactate, octopine, alanine and succinate during 16h of anoxia in the foot muscle of *Hexaplex trunculus* are shown in figures 15–18. Only alanine levels rose significantly during anoxia. The maximum alanine accumulation was observed after 12h of anoxia and was about 3.7 µmol/g wet mass. No significant changes in octopine, lactate and succinate levels were observed.

In figures 19–22 the changes in adenylates and in the energy charge in the foot muscle during 16h of anoxia of *Hexaplex trunculus* are presented. A significant de-



Figs 8–11. Changes in the concentrations of ATP, ADP, AMP and energy charge in the hepatopancreas of *Hexaplex trunculus* during various periods of anaerobiosis. 8) ATP, 9) ADP, 10) AMP, 11) energy charge. * Significantly different from the corresponding aerobic condition (t-test $P<0.05$). ** Significantly different from the corresponding aerobic condition (t-test $P<0.005$)

cline in ATP content together with a significant increase in ADP level were observed after 4h of anoxia. AMP levels remained almost unaltered. A decline in energy charge was also evident. Energy charge shifted from 0.87 to 0.72 during the first four hours of anoxia. Thereafter, it remained almost constant.

Mantle: Figures 23–25 show changes in the concentration of aspartate, glycogen and glucose in the mantle of *Hexaplex trunculus* during various periods of anaerobiosis. Among the substrates measured only aspartate showed a significant decline, being reduced to 3.4 µmol/ g wet mass during the 8 first hours of anoxia. Glycogen levels remained almost constant throughout anoxia. Glucose concentration in the mantle increased and showed a significant rise after 12 and 16h of anoxia exposure, compared to the aerobic state.

Among the metabolites presented in figures 26–29, a significant rise in lactate content was observed after 8h of anoxia. During the first four hours alanine levels decreased. Thereafter an apparent increase in alanine content was observed. This increase was not significantly different from the value of the aerobic control, owing to high variation in the alanine content of different animals. There were no significant differences in octopine and succinate content among the different periods tested.

Concerning the changes of the adenylates shown in figures 30–33, a significant decrease in ATP content was seen until the fourth hour of anoxia. Levels of ADP increased during the first eight hours, but declined thereafter again, reaching control values. No significant change in AMP concentration was observed. Energy charge declined, mainly during the first eight hours, decreasing from 0.9 to 0.73.

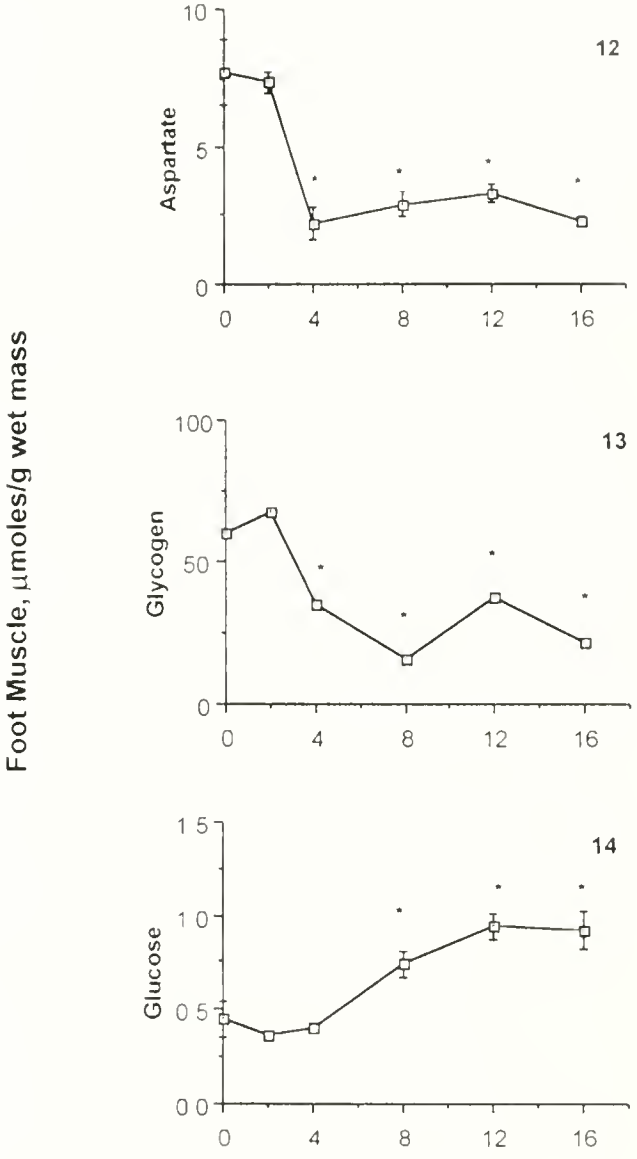
DISCUSSION

The ability of invertebrate anaerobes to sustain long periods of anoxia is mainly based on the metabolic adaptations of their tissues. These species are able to reduce their metabolic rate and at the same time to maintain

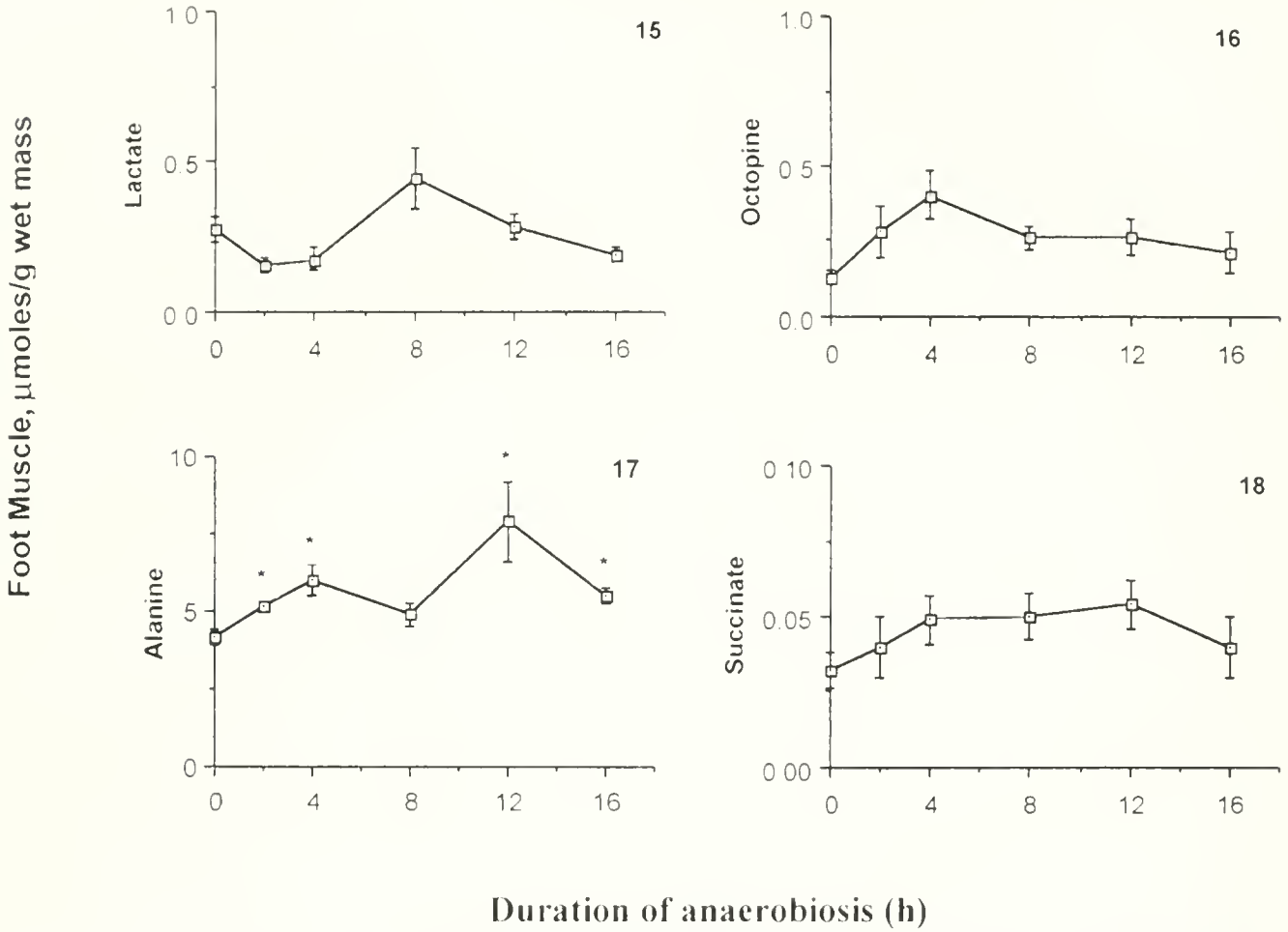
their energy reserves so as to confront the energetic needs of their tisssues. The ATP production is generally based on the anaerobic breakdown of glycogen. In contrast to mammalian systems, this anaerobic breakdown of glycogen does not lead to lactate production. Various end products accumulate during anaerobiosis depending on species, as well as on the duration of anaerobiosis. In intertidal bivalve mollusks, the main end product of the first stages of anaerobiosis is alanine, while at later stages succinate, propionate, acetate and fatty acids can be detected (de Zwaan, 1983). Hochachka and Mustafa (1972) proposed that amino acids should be an important anaerobic fuel in intertidal bivalve tissues and they put forward a metabolic map integrating the metabolism of glucose, aspartate and glutamate during anoxia The metabolic behaviour of subtidal species during anaerobiosis is almost unknown.

The results of the present study revealed that foot muscle, mantle and hepatopancreas of *Hexaplex trunculus* catabolize aspartate and accumulate alanine in response to 16h of anoxia. The pattern of metabolism differs among tissues. In the hepatopancreas, aspartate declines during the early stages of anaerobiosis and is accompanied by a simultaneous rise in alanine content (figs. 1 and 6). After this initial response, aspartate declines more slowly, while alanine accumulates up to the 16th hour of anaerobiosis, compared to the aerobic state. Glutamate, a possible end product of anaerobiosis in intertidal species, is not accumulated in the hepatopancreas of *Hexaplex trunculus* during anoxia (results not shown). A significant rise in glucose content was observed, starting from the very beginning of oxygen deprivation and rose by a factor of ten till the 16th hour of anaerobiosis (fig. 3). It could be suggested that *Hexaplex trunculus* hepatopancreas responds rapidly to anoxia by catabolising mainly aspartate and accumulating initially alanine and subsequently succinate (fig.1,6,7). Elevation of tissue glucose could not be attributed to glycogen degradation since glycogen levels showed no signs of decreasing throughout anoxia. Similarly no significant decrease in glycogen content was found in hepatopancreas, foot, and phasic adductor muscle of the cherrystone clam *Mercenaria mercenaria* (Koryean & Storey, 1983). No change in the percentage of phosphorylase in the active α form was found in the adductor muscle of *Mytilus edulis* over a time course of up to 18h of anoxia (Ebberink & Salimans, 1982).

In the foot muscle of *Hexaplex trunculus*, the response to anoxic stress is less rapid than in the hepatopancreas. This agrees with the findings of Whitman and Storey (1989), who suggested that the processes involved in anoxia induced modification of glycolytic enzymes are more rapidly initiated in non muscular than muscular tissues. A sharp decline in aspartate content is obvious after four hours of anoxia, while alanine accumulation is maximal after twelve hours of anoxia (fig. 12 and 17). The low levels of succinate did not change throughout anoxia (fig. 18). This could either suggest that the succinate pathway is not functioning in the foot muscle of *Hexaplex trunculus*, or that succinate is rapidly metabolized to another end product (i.e. propionate or acetate). Similarly, it was reported that in the subtidal marine gastropod *Nassarius reticulatus* only alanine and no succinate accumulated throughout anoxia (Wieser, 1980). The Mediterranean bivalve *Scapharca cf. cornea* Reeve, 1843 also produced no succinate during 72h of anoxia (Carpené *et al.*, 1981). However, in the foot muscle of the subtidal whelk *Nassa*



Figs 12–14. Changes in the concentrations of aspartate, glycogen and glucose in the foot muscle of *Hexaplex trunculus* during various periods of anaerobiosis. 12) aspartate, 13) glycogen, 14) glucose. * Significantly different from the corresponding aerobic condition (t-test $P<0.05$)

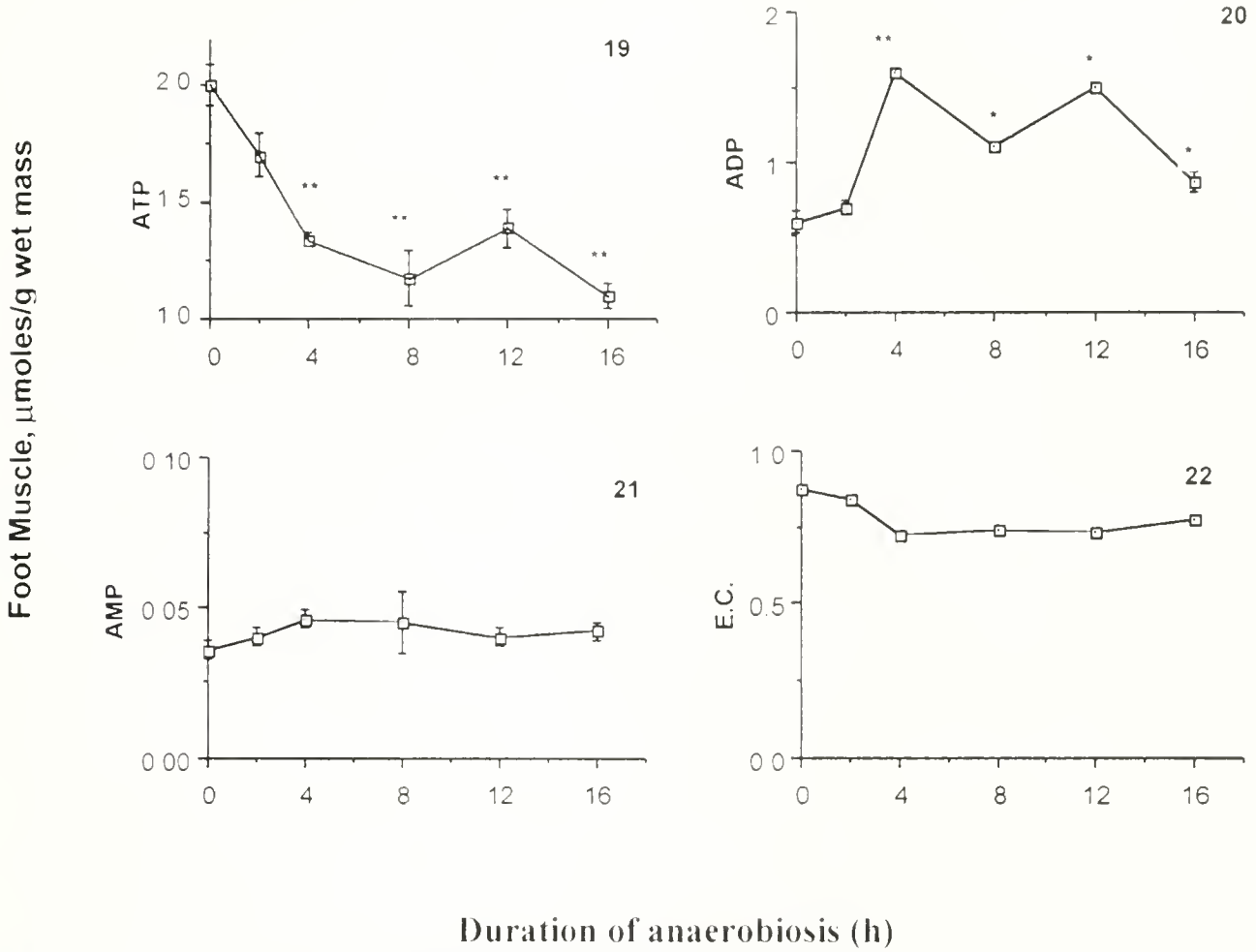


Figs 15–18. Changes in the concentrations of lactate, octopine, alanine and succinate in the foot muscle of *Hexaplex trunculus* during various periods of anaerobiosis. 15) lactate, 16) octopine, 17) alanine, 18) succinate. * Significantly different from the corresponding aerobic condition (t-test $P<0.05$).

mutabilis succinate was produced, but only in low concentrations (Gäde *et al.*, 1984). In contrast to hepatopancreas, glycogen content falls sharply after four hours of anoxia (fig. 13). The observed glycogen degradation in the foot muscle could be correlated with the continuous effort of the animal to move away from areas deprived of oxygen. The elevated glucose levels, probably derived from glycogen catabolism, could be the main metabolic substrate used to support muscular work under anaerobic conditions. No lactate and octopine accumulation was found (fig. 15, 16). Our results concur with the data presented by Kluytmans *et al.* (1983) and Gäde *et al.* (1984). It seems, therefore, that the foot muscle of *Hexaplex trunculus* shows no signs of energy stress during the first two hours of anoxia. Later, it responds to anoxia by catabolizing aspartate and glycogen and accumulating mainly alanine.

Due to the declining levels of aspartate in the mantle during anaerobiosis, aspartate appears to be the main source of energy production during anoxia. Alanine accumulation presented a somewhat different pattern of accumulation compared to the two other tissues examined (fig. 28). There was an initial decline in its level, followed by a subsequent increase up to the 16th hour of anoxic stress. However, owing to great variation in mantle alanine content among different individuals, the values did not differ from the control. Similarly, alanine did not accumulate in the mantle tissue of *Mytilus edulis* at reduced oxygen tensions, but it accumulated in the posterior adductor muscle under the same conditions (Livingstone & Bayne, 1976).

Glucose levels increased during anoxia in all three tissues examined. Glucose levels in the hepatopancreas rose from the very begining of anoxia, reaching its maximum value after 16h of oxygen deprivation where a tenfold increase in its content could be observed. However, glucose increases in foot muscle only after 8h of anoxia and in mantle tissue after 12h of anoxia. This delayed increase could be correlated with the time needed for glucose residues to be mobilized from the hepatopancreas and transferred to the foot muscle and the mantle via the hemolymph. While glucose levels in the

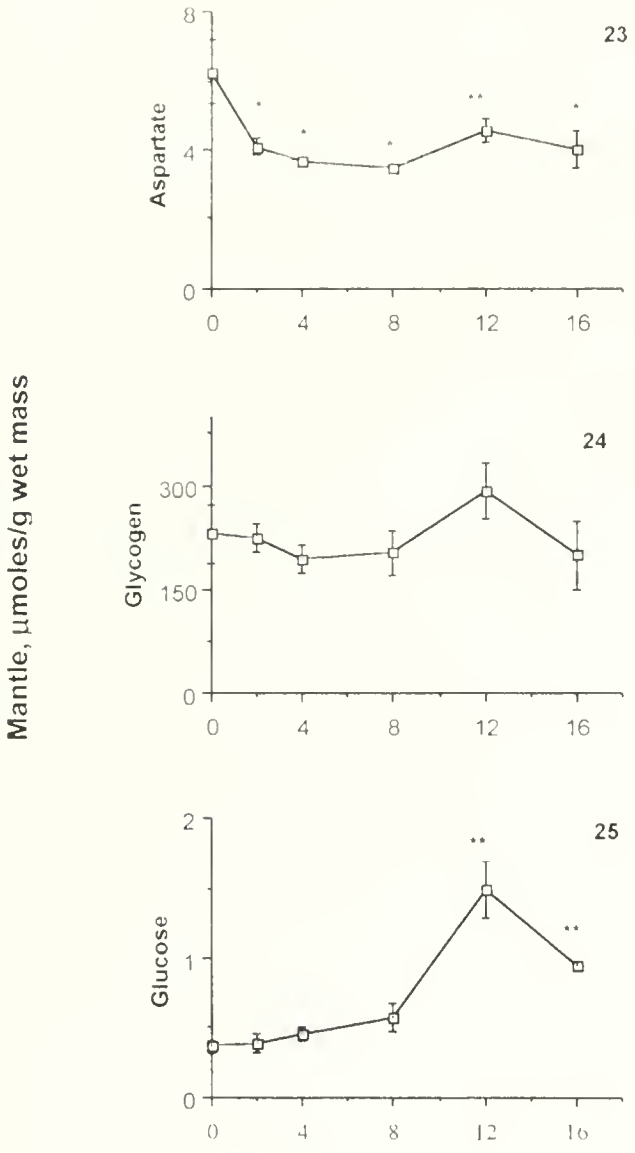


Figs 19–22. Changes in the concentrations of ATP, ADP, AMP and energy charge in the foot muscle of *Hexaplex trunculus* during various periods of anaerobiosis. 19) ATP, 20) ADP, 21) AMP, 22) energy charge. * Significantly different from the corresponding aerobic condition (t-test $P<0.05$). ** Significantly different from the corresponding aerobic condition (t-test $P<0.005$)

hepatopancreas increased by tenfold, only a twofold increase was observed in foot muscle and mantle. This suggests that glucose was synthesized in the hepatopancreas to supply other tissues and help them meet their metabolic demands during conditions of prolonged oxygen deprivation. A similar rise in glucose concentration during anoxia was observed in various tissues of the cherrystone clam, *Mercenaria mercenaria* where glucose levels doubled throughout anoxia (Korycan & Storey, 1983). In the fresh water snail *Lymnaea stagnalis* Linné, a strong and rapid hyperglycaemic response is evoked during anoxia (Wijsman *et al.*, 1988). Hemminga *et al.* (1985a) were able to prove that in *L. stagnalis* a hyperglycemic factor is released by the central nervous system during conditions of glycogen breakdown. The cerebral ganglia contain the main release sites of this factor. The ganglionectomised animals showed reduced levels of hyperglycemia associated with exposure to anaerobic conditions (Hemminga *et al.*, 1985b).

All three tissues showed a significant decrease in ATP content (figs. 8, 19, 30). In hepatopancreas and mantle tissue this decline is evident after the first two hours of anoxia, while in foot muscle a significant decline is obvious after the fourth hour. The sharp reduction in ATP levels of the hepatopancreas may in part be attributed to gluconeogenic procedures that continually consume ATP which is barely replenished, owning to the low levels of glycolysis. Only the hepatopancreas shows a significant accumulation of succinate throughout anoxia. Therefore, the succinate pathway may be activated in the tissue after the initial drop in ATP reserves. Although ATP levels decrease in foot muscle and mantle tissue, these organs still maintain a relatively high energy charge, so activation of succinate pathway may not be necessary.

In contrast to intertidal species studied so far (Zurburg & Kluytmans, 1980; Michaelidis & Beis, 1990), the succinate pathway is a route of minor importance for anaerobic energy production in mantle and foot muscle of



Figs 23–25. Changes in the concentrations of aspartate, glycogen and glucose in the mantle of *Hexaplex trunculus* during various periods of anaerobiosis. 23) aspartate, 24) glycogen, 25) glucose. * Significantly different from the corresponding aerobic condition (t-test $P<0.05$). ** Significantly different from the corresponding aerobic condition (t-test $P<0.005$).

the subtidal species *Hexaplex trunculus*. This observation can be correlated with its habitat. In general, most sublittoral mollusks can tolerate anoxia less well than intertidal mollusks. There seems to be a relationship between the habitat (and its oxygenation) and the animals anoxia tolerance. (Gäde, 1983). The production of succinate during anaerobiosis provides the animals with extra ATP, due to the coupling of the fumarate reductase system with the first phosphorylation site of the electron transport chain (Holwerda & de Zwaan, 1979; 1980; Köhler, 1976; 1980). The enhancement of the energetic efficiency of the anaerobic metabolism in these animals enables them to withstand long periods of anoxia. It seems that subtidal species have not adapted a functioning succinate pathway.

However, the question of the final electron acceptor under conditions of oxygen deprivation remains unanswered. *Hexaplex trunculus* survives anaerobiosis for 100–200h (Zs Nagy, 1971). Furthermore, the lack of succinate accumulation in its tissues after several hours of anoxia suggests that another electron acceptor, apart from O_2 and fumarate may exist. In 1971, Zs Nagy suggested that energy production in mollusks during prolonged anoxia may be realized by means of a mechanism called "anoxic endogenous oxidation". This mechanism is localized in the cytosomes and its essential point is that molecular oxygen is replaced by an internal electron acceptor, a lipochrome pigment located in the cytosomes. Furthermore, heavy pigmentation was found in the central nervous system of *Hexaplex trunculus* (Zs Nagy, 1971). Consequently, the latter process, which takes place within special cell organelles, may function for a certain period of time, in the tissues of this subtidal gastropod for production of biologically utilizable energy under conditions of oxygen deprivation. The biochemical mechanisms for such control processes warrant further investigation.

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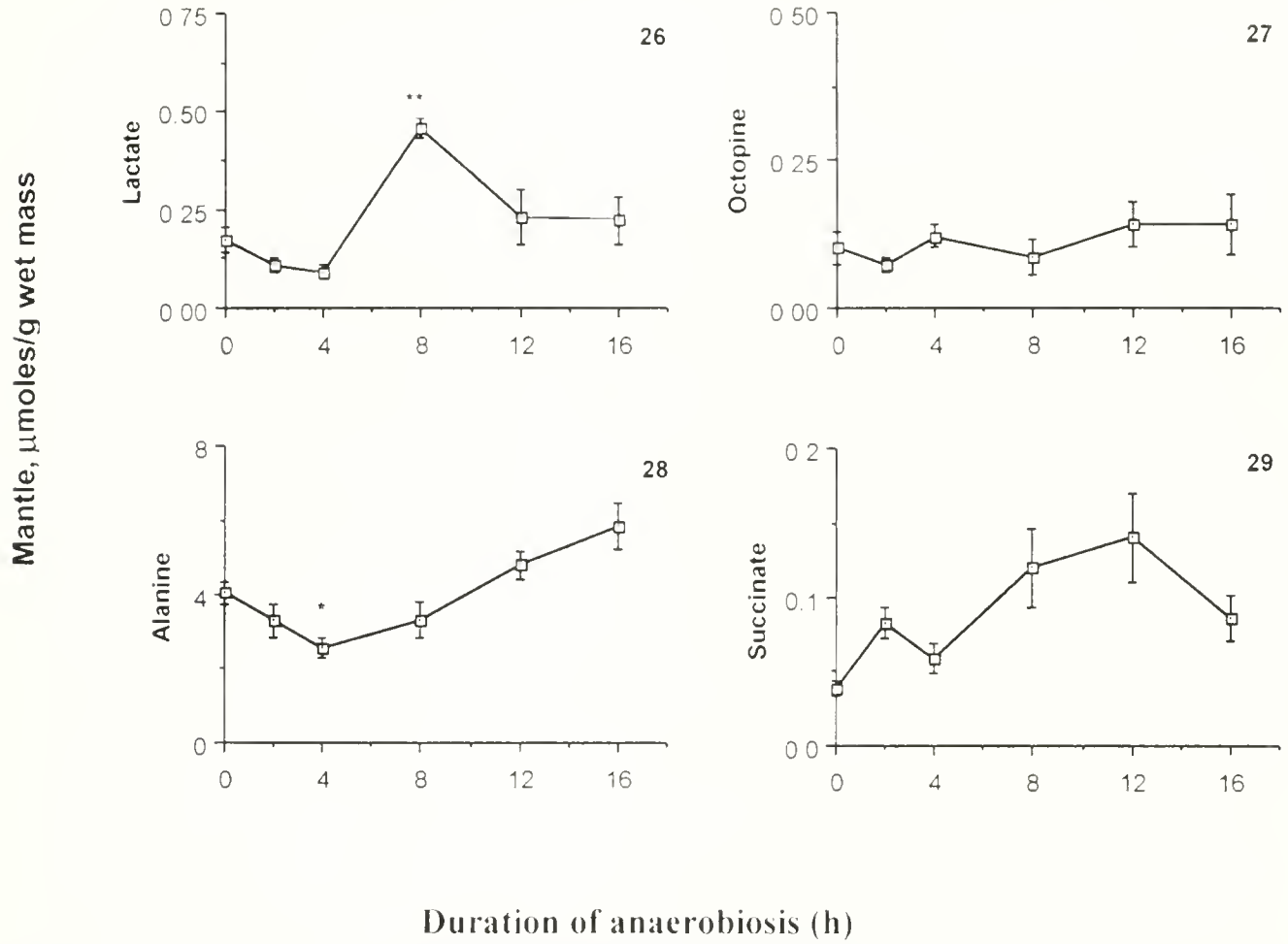

Figs 26–29. Changes in the concentrations of lactate, octopine, alanine and succinate in the mantle of *Hexaplex trunculus* during various periods of anaerobiosis. 26) lactate, 27) octopine, 28) alanine, 29) succinate. * Significantly different from the corresponding aerobic condition (t-test $P<0.05$). ** Significantly different from the corresponding aerobic condition (t-test $P<0.05$).

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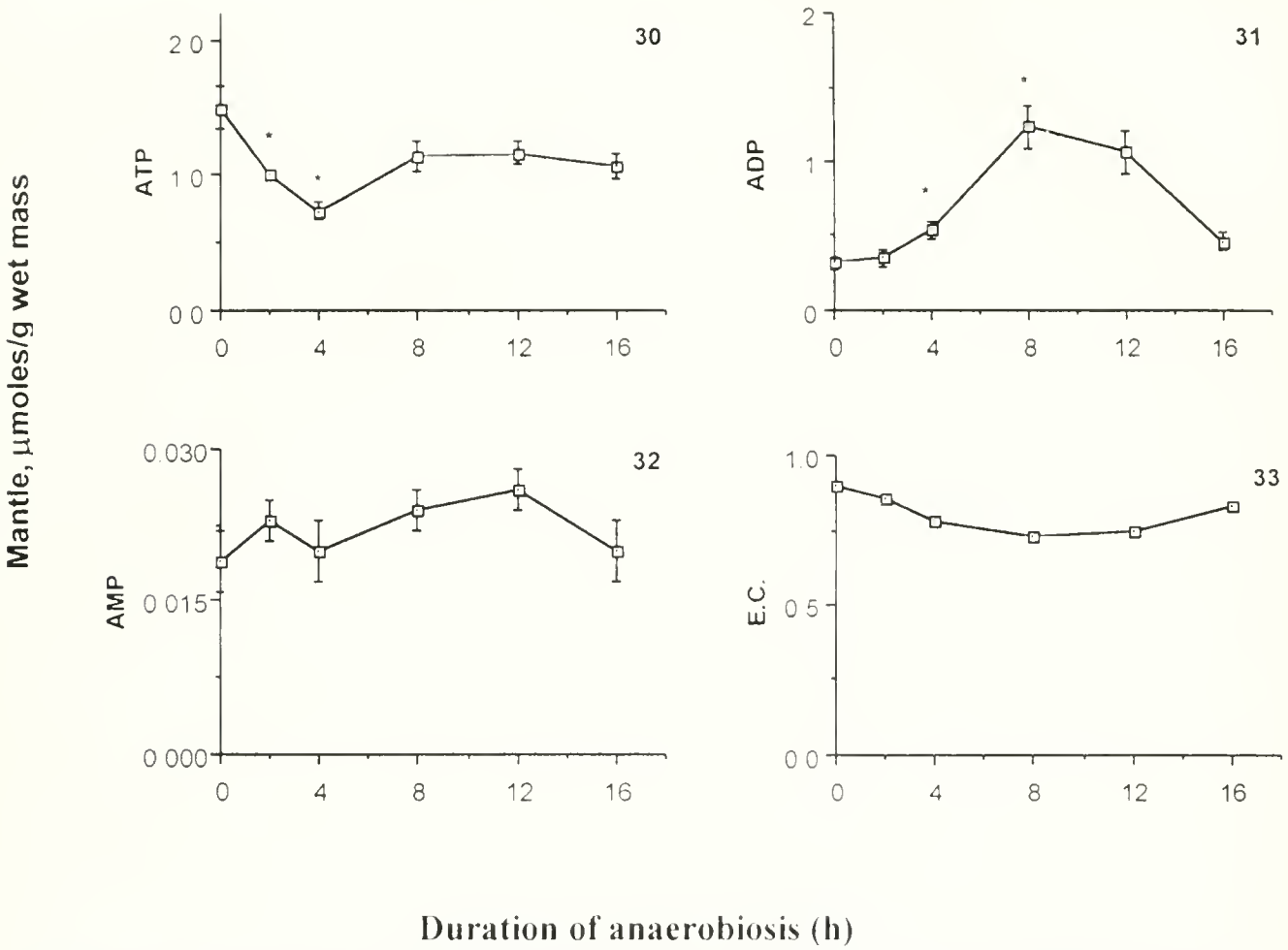

Figs 30–33. Changes in the concentrations of ATP, ADP, AMP and energy charge in the foot muscle of *Hexaplex trunculus* during various periods of anaerobiosis. 30) ATP, 31) ADP, 32) AMP, 33) energy charge. * Significantly different from the corresponding aerobic condition (t-test $P<0.05$).

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On the Identity of *Morula martensi* Dall, 1923 and Description of a New Species of *Ergalatax* from the Red Sea (Gastropoda: Muricidae: Ergalataxinae)

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ABSTRACT

Morula martensi Dall, 1923 differs from the similar species *Ergalatax margariticola* (Broderip, 1833) by having a smaller, narrower and white shell. The species erroneously identified as *Ergalatax* or *Cronia martensi* (Dall, 1923) in recent literature is named here as *Ergalatax obscura* n.sp.

Key Words. Gastropoda, Muricidae, *Morula martensi*, new species.

INTRODUCTION

Martens (1874:95, pl. 5, fig. 49) identified and illustrated a shell from the Hausknecht collection as *Purpura (Ricinula) siderea* Reeve, 1846. Examination of the type material of *Ricinula siderea* (3 syntypes BMNH 1968478, type locality: Philippines, ex coll. H. Cuming), revealed that it is a buccinid, and not the species illustrated by Martens, which Dall (1923:304) subsequently named *Morula martensi*. The seven specimens examined by Martens, all from the Persian Gulf, are stored in the Museum für Naturkunde, Berlin. Martens' original figure is here reproduced (fig. 2), and the actual specimen figured (figs. 12, 13).

Martens' description, figure, and comparisons with *Purpura undata* (Chemnitz, 1795:pl. 192, fig. 1852) [= *Ergalatax margariticola* (Broderip, 1833)], my re-examination of the specimens of the Hausknecht collection and comparison with specimens from Qatar (coll. R. Houart), reveal that this species is similar to *E. margariticola*. The shells from Oman and the Persian Gulf are white with black blotches on the spiral cords (figs. 12–15), and differ from *E. margariticola*, which has a broader, more darkly pigmented shell. Specimens from Oman were illustrated by Bosch and Bosch (1982:95, 1989:60) as *Cronia konkanensis* (Melvill, 1893), which, however, is probably a distinct species, more closely related to *Thais muricina* (Blainville, 1832) and *T. marginatra* (Blainville, 1832), both classified in Rapaninae. If the populations from the Persian Gulf prove to be only an ecological form of *E. margariticola*, then *E. martensi* (Dall, 1923) will become a junior synonym of that species. *Ergalatax martensi* was reported to be a synonym of *E. contracta* (Reeve, 1846) by Houart (1995:251). It is here considered a distinct species.

Three distinct species with similar gross morphology have been confused in the recent literature. *Ergalatax martensi* (Dall, 1923), from Oman and the Persian Gulf, is closely related to but probably distinct from *E. margariticola* (Broderip, 1833); *Ergalatax obscura*, new species, from the Gulf of Aden, the Red Sea, the Gulf of Aqaba and the Mediterranean coast of Turkey, is a distinct species identified incorrectly as *Cronia* (or *Ergalatax*) *martensi* (Dall) in recent literature; and *Thais konkanensis* (Melvill, 1893), from the Indo-West Pacific, which is closely related to *T. muricina* (Blainville, 1832) and *T. marginata* (Blainville, 1832).

My researchs were incomplete when I received photographs and material for identification from Turkey, from G. Buzurro and W. Engl. At the time, I provisionally identified the new Mediterranean immigrant as *Ergalatax martensi*, and it was reported as such by Buzurro, Engl and Tümtürk (1995) and by Engl (1995). It is now evident that *E. martensi* is confined to Oman and the Persian Gulf, and that the Turkish species is *E. obscura* n.sp.

SYSTEMATICS

Order Neogastropoda Thiele, 1929
Superfamily Muricoidea Rafinesque, 1815
Family Muricidae Rafinesque, 1815
Subfamily Ergalataxinae Kuroda & Habe, 1971
Genus *Ergalatax* Iredale, 1931

Ergalatax Iredale, 1931:231. Type species (by original

designation): *Ergalatax recurrens* Iredale, 1931; off Sydney Harbour, New South Wales, Australia.

Ergalatax martensi (Dall, 1923)
(figs. 2, 12–15)

Morula martensi Dall, 1923:304, new name for *Morula siderea* von Martens,1874, not Reeve, 1846.
Cronia konkanensis—BOSCH & BOSCH, 1982:95, text fig.; SMYTHE, 1982:60, pl. 1, fig. i, BOSCH & BOSCH, 1989: 60, text fig. (not *Ricinula konkanensis* Melvill, 1893).

NOT *Cronia martensi*—SHARABATI, 1984:pl. 19, fig. 9, SINGER & MIENIS, 1991b:58, fig. 19 (in part); COULOMBEL, 1994:73, text figs (=*Ergalatax obscura* n.sp.).
NOT *Ergalatax martensi* BUZURRO, ENGL & TüMTüRK, 1995: 17, text fig.; ENGL,1995. 46, fig. 10 (= *Ergalatax obscura* n.sp.).

Deseription: Shell up to 26.5 mm in length at maturity, slender, squamous. Spire high with 6 weakly convex, shouldered teleoconch whorls. Suture adpressed. Protoconch eroded in all specimens examined. Axial sculpture of teleoconch whorls consisting of high, strong, nodose ribs, producing blunt knobs at intersection with spiral cords. 9 or 10 ribs on first and second whorls, 8–10 on third, 9–12 on fourth and fifth, 7–10 on last whorl. Ribs more strongly developed at shoulder. Other axial sculpture of numerous growth lamellae. Spiral sculpture of low, squamous cords of various strength. Usually 13 or 14 cords on last whorl, and 6 additional, smaller cords on shoulder. Aperture narrow, ovate. Columellar lip smooth, occasionally with 1 or 3 weak folds abapically. Lip adherent. Anal notch narrow, deep. Outer lip crenulate, with 6–8 weak, elongate denticles within. Siphonal canal short, broad, open. White, with primary spiral cords, or knobs only, topped with dark brown or black. Aperture glossy white. Operculum dark brown with subterminal nucleus. Radula unknown.

Type material: Lectotype (here selected), the specimen figured by Martens (1874) as *Purpura (Ricinula) siderea*, not Reeve, 1846, and 6 paralectotypes ZMB 21596.

Type loeality: Persian Gulf, here designated.

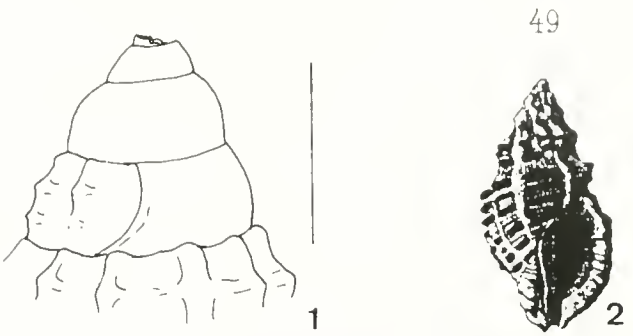
Other material examined: QATAR: Doha, landing stage, coll. R. Houart (10).

Distribution: Oman and the Persian Gulf.

Remarks: As stated above, the shell is close to *Ergalatax margariticola* (Broderip, 1833), but differs in being usually smaller relative to the number of teleoconch whorls, narrower, and in having a white ground color and a white, glossy aperture, instead of cream or light brown in *E. margariticola*.

Ergalatax obscura n.sp.
(Figs 1, 3–8)

Cronia martensi—SHARABATI, 1984 pl 19, fig 9, 9a, 9b; SINGER & MIENIS,1991b: 58, fig. 19; COULOMBEL, 1994 73, text figs) (not *Morula martensi* Dall, 1923).
Drupella rugosa SINGER & MIENIS, 1991a: 18, fig. 6 (not *Murex rugosus* Born,1778).
Cronia cf *konkanensis*—GIUNCHI & TISSELLI, 1995: 8, text figs.
Ergalatax martensi—BUZURRO, ENGL & TüMTüRK, 1995: (no pag.), text fig; ENGL, 1995: 46, fig. 10 (not *Morula martensi* Dall, 1923).



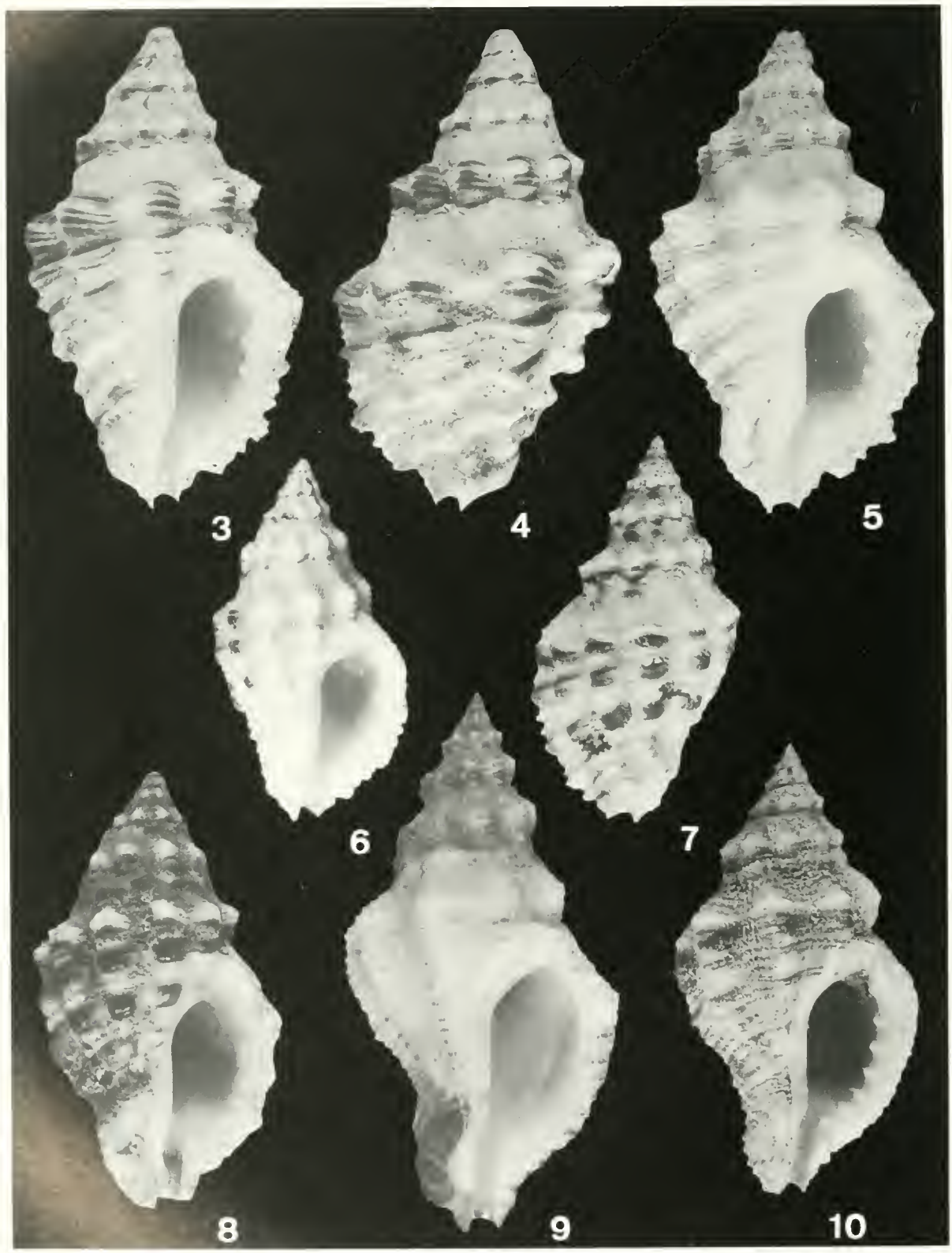
Figures 1, 2. 1. Protoconch of *Ergalatax obscura* n.sp. (scale bar: 0.5 mm). **2.** Fig. 49 of Martens (1874), as *Purpura siderea* (Reeve).

Description: Shell medium sized for the genus, up to 25.5 mm in length at maturity, heavy, stout. Spire high with 3+ protoconch whorls (partially broken), and up to 7 broad, strongly shouldered teleoconch whorls. Suture adpressed. Protoconch conical, acute, whorls smooth. Axial sculpture of teleoconch whorls consisting of high, rounded, nodose ribs: 10 or 11 from first to penultimate whorl, 6 to 8 on last whorl. Spiral sculpture of high, strong, primary, secondary, and tertiary cords. Sculpture forming high, nodose knobs at intersection of spiral cords and axial ribs. Aperture relatively small, ovate. Columellar lip with 2 or 3 weak knobs abapically, rim adherent. Anal notch broad, moderately deep. Outer lip weakly crenulate, with 7 strong, elongate denticles within. Siphonal canal short, broad, broadly open. Milky-white, creamy-white, or tan, usually with some light to dark brown coloured spiral cords on shoulder and on more prominent nodes. Aperture cream or pale yellow within. Operculum ergalataxine, with subterminal nucleus. Radula unknown.

Type material: RED SEA: Djibouti, Perim, Strait of Bab el Mandeb. Holotype MNHN; paratypes: MNHN (4), coll. R. Houart (1); GULF OF ADEN: Djibouti, Obock. Paratypes: MNHN (9); Yemen, Aden. Paratypes: MNHN (4), AMS C. 309658 (1), NMNZ M.270540 (1), NM L1647. T1336 (1), coll. R. Houart (1).

Type locality: Red Sea, Djibouti, Perim, Strait of Bab el Mandeb.

Other material examined: GULF OF ADEN (no other data): coll. R. Houart (3); RED SEA: Massawa, MNHN (2); no other data, coll. R. Houart (1); GULF OF AQABA: Egypt, Sharm El Sheik, coll. R. Houart (2); Israël, Eilat, coll. R. Houart (3).



Figures 3–8. *Ergalatax obscura* n.sp. **3–4.** Holotype MNHN, Djibouti, Perim, Strait of Bab el Mandab, 24.2mm. **5.** Paratype MNHN, Aden, Yemen, 24.2 mm. **6.** Sharm El Sheik, 20 mm, coll. R. Houart. **7.** Paratype MNHN, Aden, Yemen, 19.2 mm. **8.** Paratype MNHN, Gulf of Aden, Djibouti, Obock, 23 mm. **Figures 9, 10.** *Ergalatax contracta* (Reeve, 1846). **9.** New Caledonia, 31.9 mm, coll. R. Houart. **10.** Sri Lanka, 22.8 mm, coll. R. Houart.

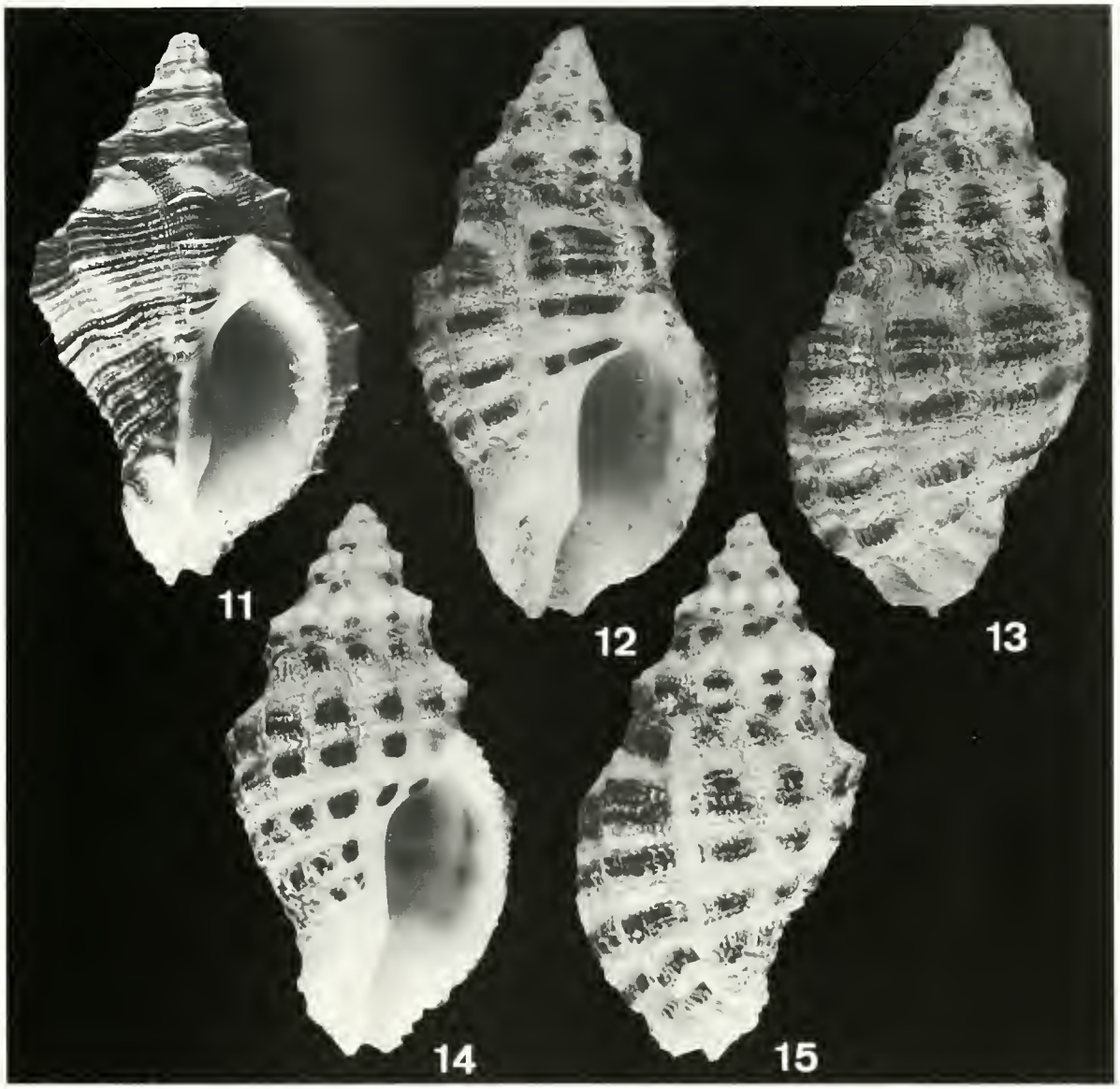


Figure 11. *Ergalatax heptagonalis* (Reeve, 1846), 31 mm, syntype BMNH 1968476. **Figures 12–15.** *Ergalatax martensi* (Dall, 1923). **12–13.** Persian Gulf, Hausknecht coll., illustrated by Martens (1874), 21.4 mm, Museum für Naturkunde, Berlin n° 21596. **14–15.** Persian Gulf, Qatar, 23.2 mm, coll. R. Houart.

Distribution: Gulf of Aden, Red Sea, and Gulf of Aqaba. Mediterranean: Turkey, from Iskenderun to Tasucu (Buzurro, Engl & Tümtürk, 1995; Engl, 1995; Giunchi & Tisselli, 1995).

Etymology: obscurus—(Latin) enigmatic. [indistinct is a more literal translation].

Remarks: *Ergalatax obscura* n.sp. differs from *E. martensi* in having a smaller, more strongly shouldered shell with broader, less numerous axial ribs, and more adpressed suture. It is milky white, cream or tan with light or dark brown blotches, with a cream or pale yellow aperture, while *E. martensi* is white with dark brown or black blotches, with a glossy white aperture. *Ergalatax obscura* n.sp. differs consistantly from the similar *E. contracta* (Figs 9–10) in its stouter shell with stronger, more pronounced, and more nodose axial ribs, broader spiral cords, shorter and relatively broader siphonal canal, and more adpressed suture.

I am not aware of intermediate forms between *E. obscura* and *E. contracta*, and no specimen of *E. obscura* has been found elsewhere in the extensive material of *E. contracta* examined from localities throughout the Indo-West Pacific. However, there are two typical specimens of *E. contracta* in the lot containing the holotype of *E. obscura*.

From *E. heptagonalis* (Reeve, 1846) (Fig. 11), *E. obscura* differs in its higher, more pronounced, and more nodose axial ribs, and in its broader spiral cords.

Although the shell of *E. obscura* seems to be close to

some forms of *Drupella rugosa* (Born, 1778), a Rapaninae, it differs in being stouter, in having a lower spire, fewer, broader spiral threads, and a more adpressed suture. The operculum of *E. obscura* is typically ergalataxine with a subterminal nucleus, compared to the typically rapanine "D" shaped operculum of *D. rugosa*, with lateral nucleus.

ACKNOWLEDGEMENTS

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Calusacypraea, A New, Possibly Neotenic Genus of Cowries (Gastropoda: Cypraeidae) from the Pliocene of Southern Florida

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ABSTRACT

The new cypraeid genus *Calusacypraea* n. gen. is described from the Okeechobean Sea region of Pliocene southern Florida. This new genus is unusual among American fossil cowries in that it bears many juvenile shell characters into adulthood and possibly represents a neotenic evolutionary offshoot of *Siphocypraea*. Based on paleoecological inferences, *Calusacypraea* was an inhabitant of shallow water lagoonal and estuarine environments and became extinct at the end of the Pliocene with the obliteration of the Okeechobean lagoonal systems. Three new *Calusacypraea* species are described: *C. briani* n. sp. (from Petuch Unit 7), *C. duerri* n. sp. (type of the genus, from Petuch Unit 10), and *C. tequesta* n.sp. (from Petuch Unit 4). The previously described species, *C. sarasotaensis* (Petuch, 1994), is included in this new genus.

Key words: Cypraeidae, *Calusacypraea*, Pliocene, Florida.

INTRODUCTION

Southern Florida has long been known to house the largest Pliocene cowrie fauna found anywhere in the United States. The works of Heilprin (1886), Mansfield (1931), Olsson and Petit (1964, 1968), Parodiz (1988), and Petuch (1986, 1991, 1994), altogether, show that the ecosystems of the Okeechobean Sea region of Pliocene Florida (Petuch, 1994:26) contained at least 23 different cowrie species. With the exception of one species of *Pseudozonaria*, all were thought to belong to a single endemic genus, *Siphocypraea* Heilprin, 1886. The southern Caribbean Gatunian cowries previously placed in *Siphocypraea* are now placed in *Barycypraea* (*Muracypraea*). This classic Okeechobean genus radiated into numerous neritic habitats during the late Pliocene, but became extinct in the early Pleistocene. The genera *Macrocypraea* and *Luria* later replaced *Siphocypraea* in the local reef communities (Petuch, 1994:11).

Recently, studies of new collections of fossil cowries from the Quality Aggregates, Inc., quarries at Sarasota (housed at Florida Atlantic University) have shown that there existed a second endemic cowrie genus in the Pliocene Okeechobean Sea. This previously-overlooked genus, here named *Calusacypraea*, bears many juvenile characters into adulthood (so much so that I discarded numerous choice adult specimens, thinking that they were merely juvenile or subadult *Siphocypraea* species!). This new, possibly neotenic, genus and its new species are described and discussed here.

SYSTEMATICS

Superfamily Cypraeoidea Rafinesque, 1815
Family Cypraeidae Rafinesque, 1815
Genus *Calusacypraea* new genus

Diagnosis: Cypraeid shells of average to large size, ranging from 35 to 70 mm in length, extremely inflated, thin, delicate, bulliform; apices characteristically very depressed, forming distinct apical pit; posterior edge of lip typically highly-developed, greatly-projecting beyond plane of spire; columellar side of apical area poorly-developed, only slightly projecting beyond plane of spire; anterior extremities poorly developed, without distinct projecting beaks; ends of anterior extremities do not extend beyond end of anterior canal, producing rounded, blunt, sheared-off appearance; in some species, anterior extremity on labial side almost absent, with extremity blending into rounded end of lip and giving shell juvenile appearance; bases of shells very rounded; margins of shells poorly-developed, rounded, with only thin enamel deposits; anterior canal thickened, bordered by prominent enamel collar; apertures proportionally narrow, variably widening toward anterior end; columellar teeth proportionally small, thin, and narrow, extending along length of columella; some species with row of obsolete, secondary teeth developed along anterior end of columella; labial teeth well-developed, confined to edge of lip; fossula nonexistent; color pattern (when preserved) composed of numerous small, closely-spaced dots on dorsum.

Type Species: *Calusacypraea duerri* Petuch, new species, lower Pinecrest Beds (Petuch Unit 10), Tamiami

Formation, Piacenzian Pliocene of southern Florida, U.S.A.

Other Species Assigned to *Calusacypraea*: *Calusacypraea briani* Petuch, new species, Pinecrest Beds (Petuch Unit 7), Tamiami Formation; *Calusacypraea sarasotaensis* (Petuch, 1994), Pinecrest Beds (Petuch Unit 3), Tamiami Formation; *Calusacypraea tequesta* Petuch, new species, Pinecrest Beds (Petuch Unit 4), Tamiami Formation.

Stratigraphic Range: At present, known only from the Piacenzian Pliocene of southern Florida (Pinecrest Beds, Tamiami Formation).

Etymology: Named for the Calusa Indian tribe of pre-Columbian southern Florida.

Remarks: *Calusacypraea* is most closely related to the sympatric genus *Siphocypraea* and probably represents a neotenic evolutionary offshoot of this sister group. The new genus differs from *Siphocypraea* in consistently having much thinner, more delicate, and much more inflated shells with a distinctly juvenile appearance (an example of neoteny?). The anterior extremities of *Siphocypraea* are well-developed and flange-like, with most species having the extremities formed into large, greatly-projecting beaks that extend beyond the end of the siphonal canal (Figure 9). In *Calusacypraea* the anterior extremities are distinctly truncated and poorly developed, never extending beyond the end of the siphonal canal, a morphology generally seen only in juvenile cowries. In some species of *Calusacypraea* (such as *C. sarasotaensis*) the extremities are asymmetrically developed, with the labial extremity being virtually unformed and blending into the curvature of the lip, much as in a juvenile.

The greatest differences between *Calusacypraea* and *Siphocypraea* are seen in the posterior area of their shells. In *Siphocypraea*, the posterior extremities are well-developed and symmetrical, with the columellar extremity projecting as much or nearly as much as the labial extremity and characteristically forming a deep, narrow, and curved apical sulcus (Figure 11). In *Calusacypraea* the columellar posterior extremity is nearly obsolete, being represented by only a thin, angled, bladelike keel. Unlike *Siphocypraea*, *Calusacypraea* species lack the curved, narrow apical sulcus, having, instead, a proportionally small, sharply-defined, deeply-impressed apical pit (Figure 10).

Ecologically, *Calusacypraea* species appear to have occupied a different niche than did *Siphocypraea* species. Without exception, all four known species of the new genus have only ever been found in muddy-sand, extreme nearshore facies of the Pinecrest Beds. These depositional environments imply estuarine conditions, and *Calusacypraea* may have represented a neotenic offshoot of *Siphocypraea* that had evolved to live in the extensive brackish water lagoons (such as the paleoestuary of the proto-Myakka River) that fringed the entire western coast of the Pliocene Floridian peninsula (Petuch, 1994, Fig. 10). With the onset of the late Pliocene glacioeustatic regressive sequences, these estuarine environments were obliterated and the ecologically-narrow genus became extinct.

The descriptions of three new *Calusacypraea* species are given here, along with the description of the only previously-known species, *C. sarasotaensis* (Petuch, 1994). The holotypes are deposited in the Invertebrate Paleontology collections of the Florida Museum of Natural History, University of Florida, Gainesville, Florida, and bear UF numbers.

Calusacypraea briani new species
(figures 1, 2)

Description: Basic morphology as for genus; shell large for genus, elongated and subcylindrical; aperture narrow, widening slightly at anterior end; columellar lip with 22 small, narrow teeth; columellar teeth sub-obsolete toward posterior end, becoming stronger and better-developed toward anterior end; outer lip with 26 small but well-developed teeth; base of shell rounded; margins poorly developed; apical pit deep, surrounded by raised apical collar; posterior columellar extremity small but well-developed, narrow and bladelike.

Type Material: Holotype, UF 68248, length 73 mm, width 43 mm; 2 paratypes, lengths 75 mm and 72 mm, Graves Museum of Archaeology and Natural History, Dania, Florida; 3 paratypes, lengths 75 mm, 73 mm, and 68 mm, collection of the author, Florida Atlantic University.

Type Locality: Pinecrest Beds Fauna (Petuch Unit 7), Tamiami Formation, in Phase 7 pit, Quality Aggregates, Inc., Sarasota, Sarasota County, Florida.

Remarks: *Calusacypraea briani* is the most elongated and cylindriform species in *Calusacypraea*. It is most similar to the older *C. duerri* from Petuch Unit 10, but differs in having a much narrower aperture, in having proportionally larger and coarser teeth on the outer lip, and in having smaller and less elongated teeth on the columellar lip. The posterior columellar extremity of *C. briani* is also better-developed and larger than that of *C. duerri*, producing a much more distinct posterior sulcus.

Calusacypraea briani was collected from sediments that indicate a very shallow, quiet, intertidal mud flat

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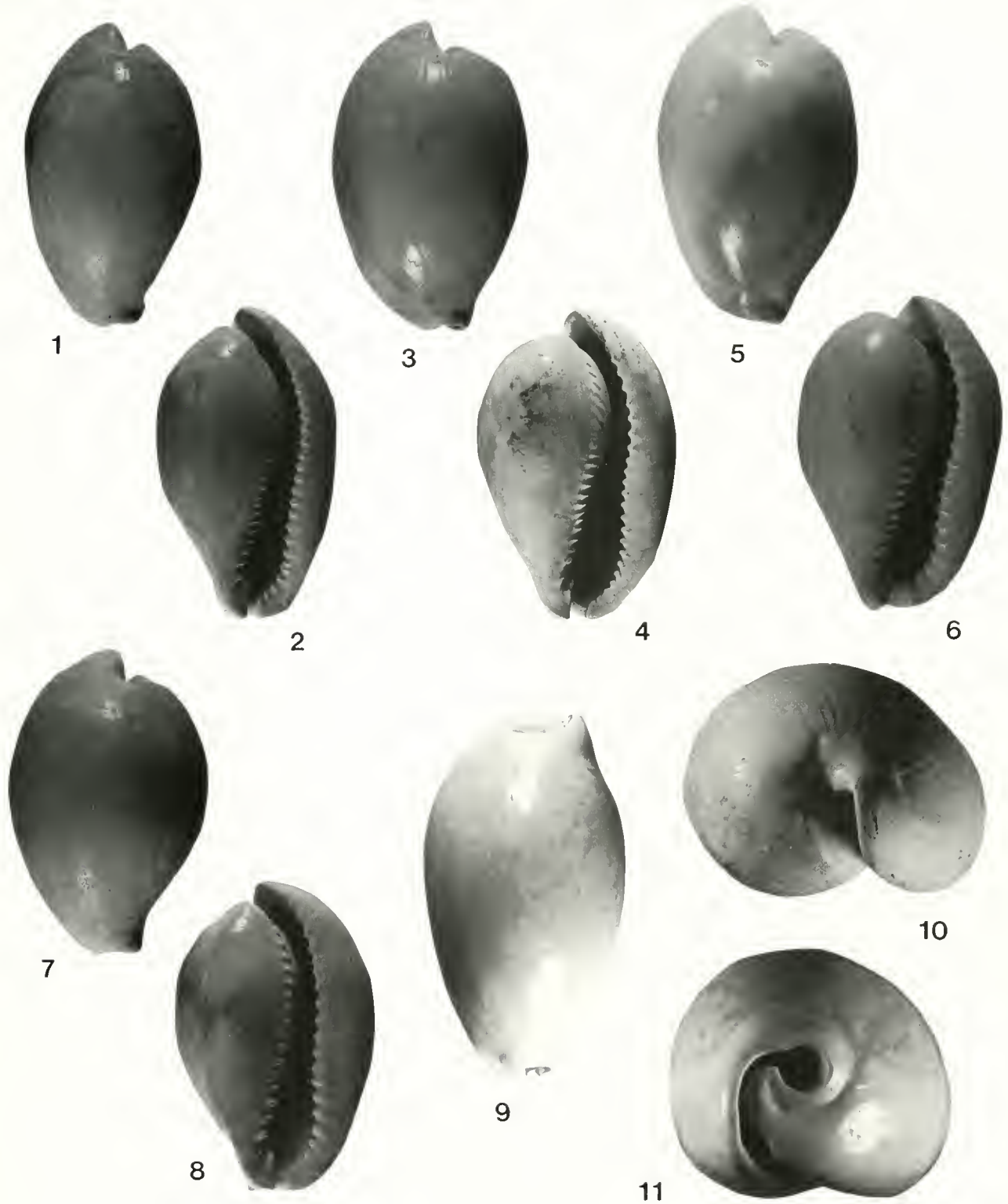
Figures 1–11. Species of *Calusacypraea*, new genus, from the coastal lagoonal environments of the Pliocene Okeechobean Sea. **1,2.** *Calusacypraea briani*, new species, holotype (length 73 mm), Pinecrest Beds Fauna (Petuch Unit 7), Tamiami Formation. **3,4.** *Calusacypraea duerri*, new species, holotype, length 64 mm, Pinecrest Beds Fauna (Petuch Unit 10), Tamiami Formation. **5,6.** *Calusacypraea sarasotaensis* (Petuch, 1994), length 42 mm, specimen from the Pinecrest Beds Fauna (Petuch Unit 3), Tamiami



Formation, APAC pit, Sarasota. **7,8.** *Calusacypraca tequesta*, new species, holotype, length 73 mm, Pinecrest Beds Fauna (Petuch Unit 4), Tamiami Formation. **9.** *Siphocypraca problematica* Heilprin, 1886, length 56 mm, specimen from the Caloosahatchee Fauna, Okeechobee Formation, in the Cochran Pit, La Belle, Hendry County. Type species of *Siphocypraca* Heilprin, 1886. **10.** Apical view of *Calusacypraca duerri*, new species (type species of *Calusacypraca*), showing details of apical pit morphology. **11.** Apical view of *Siphocypraca problematica*, showing details of apical sulcus morphology.

environment and was found with other estuarine species such as *Echinofulgur dalli* Petuch, 1994, *Cymatophos lindae* Petuch, 1991, and *Busycon tropicalis* Petuch, 1994

Etymology: Named for my son, Brian N. Petuch, one of my best field assistants.

Calusacypraea duerri new species
(figures 3, 4)

Description: Basic morphology as for genus; shell very inflated, rounded, ovate; aperture wide, flaring toward anterior end; columellar lip with 24 small, narrow, and elongated teeth; posterior columellar teeth less developed than anterior teeth, frequently bifurcated; outer lip with 23 small teeth; base of shell rounded; margins poorly developed; apical pit deep; posterior columellar extremity small, low, poorly-developed.

Type Material: Holotype, UF 68249, length 64 mm, width 40 mm; 3 paratypes, 72 mm, 66 mm, and 65 mm, Graves Museum of Archaeology and Natural History, Dania, Florida; 3 paratypes, lengths 70 mm, 65 mm, and 61 mm, collection of the author, Florida Atlantic University; 1 paratype in the collection of Mr. Richard Duerr, Hollywood, Florida.

Type Locality: Pinecrest Beds Fauna (Petuch Unit 10), Tamiami Formation, in Phase 6 pit, Quality Aggregates, Inc., Sarasota, Sarasota County, Florida.

Remarks: *Calusacypraea duerri*, the type species of the genus, is most similar to the younger and stratigraphically-higher *C. sarasotaensis* (Petuch, 1994), but differs in being a much larger shell with more numerous and better-developed columellar and labial teeth. The apical pit of *C. duerri* is deeper and more impressed than that of *C. sarasotaensis*, and the posterior columellar extremity of the new species is much lower and more poorly-developed than that of the younger, descendant species.

Calusacypraea duerri was an inhabitant of a muddy-sand substrate, shallow water ecosystem dominated by the large bivalves *Mercenaria tridacnoides* (Lamarck, 1818), *M. ochlockoneensis* (Mansfield, 1932), and *M. rileyi* (Conrad, 1838), and classic estuarine gastropods such as the melongenids *Tropochasca petiti* Olsson, 1967, *Echinofulgur cannoni* Petuch, 1994, and *Melongena taurus* Petuch, 1994, and large busyconids such as *Busycon filosum* Conrad, 1862, *B. tritonis* (Conrad, 1867), *B. pachyus* Petuch, 1994, *Sinistrofulgur hollisteri* Petuch, 1994, and *S. grabaui* Petuch, 1994.

Etymology: The new taxon honors Mr. Richard Duerr of Hollywood, Florida, who collected the holotype in Quality Aggregates Phase 6 pit.

Calusacypraea sarasotaensis (Petuch, 1994)
(figures 5, 6)

Original Description (from Petuch, 1994:271, as *Siphocypraea sarasotaensis*): "Shell small for genus, rounded, very inflated and bulliform; base of shell rounded, margins not produced; aperture proportionally very wide and open, becoming widest at anterior end; columellar lip with 14 small, poorly-developed teeth; outer lip with 19 small teeth; posterior sulcus poorly-developed, open, curving slightly to the left; extremities poorly-developed, very rounded; fossula nonexistent."

Type material: Holotype, UF66226, length 40 mm, width 18mm.

Type Locality: Pinecrest Beds Fauna (Petuch Unit 3), Tamiami Formation in APAC pit, Sarasota, Sarasota County, Florida.

Remarks:
Although originally described as coming from Petuch Unit 6, *Calusacypraea sarasotaensis* is now known to occur much higher stratigraphically, in Petuch Unit 3. The genus *Calusacypraea* becomes extinct after Unit 3 time, and *C. sarasotaensis* is the last-living member of its genus. It is also the smallest *Calusacypraea* species, averaging a length of only one-half that of the other three congeners. *Calusacypraea sarasotaensis* most closely resembles the much older, stratigraphically lower *C. duerri* from Petuch Unit 10, but differs in having a smaller and more rotund shell, fewer and coarser labial and columellar teeth, and a better-developed and more prominent posterior columellar extremity.

Colonies of *C. sarasotaensis* have been collected in muddy-sand facies of Unit 3 along with characteristic estuarine species such as *Calophos nanus* Petuch, 1994, *Echinofulgur helenae* Olsson, 1967, and *Littorina lindae* Petuch, 1994.

Etymology: Named for Sarasota County, the general area of the type locality.

Calusacypraea tequesta new species
(figures 7, 8)

Description: Basic morphology as for genus; shell very inflated, bulliform, large for genus; aperture proportionally wide, becoming wider and more open toward anterior end; columellar lip with 19 large, prominent teeth; some columellar teeth bifurcate; outer lip with 22 large and prominent teeth; base of shell rounded; margins poorly-developed accept in area bordering anterior end, where they become flattened and sharp-angled; apical pit very deep; posterior columellar extremity large and well-developed, thin and bladelike.

Type Material: Holotype, UF68250, length 73 mm, width 47 mm; 1 paratype, length 75 mm, Graves Museum of Archaeology and Natural History, Dania, Florida; 2 paratypes, lengths 75 mm and 72 mm, collection of the author, Florida Atlantic University.

Type Locality: Pinecrest Beds Fauna (Petuch Unit 4), Tamiami Formation, in APAC pit, Sarasota, Sarasota County.

Remarks: *Calusacypraea tequesta* is most similar, especially in its inflated, bulliform shell shape, to *C. duerri*

from Petuch Unit 10. The new species differs from the older, stratigraphically lower *C. duerri* in being a larger shell, in having fewer, larger, and coarser labial and columellar teeth, and in having better-developed and more flattened margins bordering the anterior end. *Calusacypraea tequesta* has the coarsest dentition of the four known species of *Calusacypraea*. This new species is a component of the rich estuarine fauna found in Petuch Unit 4 in the Sarasota quarries ("Black Layer"), where it is collected with *Siphocypraea metae* Petuch, 1994, *Pyrazisinus scalinus* (Olsson, 1967), *P. lindae* Petuch, 1994, *Cerithidea lindae* Petuch, 1994, *Bulla sarasotaensis* Petuch, 1994, *Melongena draperi* Petuch, 1994, and *Echinofulgur jonesae* Petuch, 1994.

Etymology: Named for the Tequesta Indian tribe of pre-Columbian southern Florida.

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Taxonomic Notes on South African Deep-Sea Conoidean Gastropods (Gastropoda: Conoidea) described by K.H. Barnard, 1963

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ABSTRACT

Type specimens of ten species of deep-sea conoidean gastropods from South Africa described by Barnard in 1963 are described and illustrated. Lectotypes are designated for those species represented by syntype series. A new genus, *Abyssothauma*, is established for *Moniliopsis psilarosis* Barnard, 1963.

Key words: Conoidea, South Africa, deep-sea, type specimens.

INTRODUCTION

In 1963, K. H. Barnard described a collection of South African deep-sea mollusks obtained at lower bathyal to upper abyssal depths. Most of the new species described were conoidean gastropods. Unfortunately, the new species were rather sketchily and often inadequately illustrated, which hampers their identification and comparison with other deep-sea species. None of Barnard's species of deep-sea conoidean gastropods were subsequently figured, and most were not subsequently mentioned by other authors.

There are no reviews of the deep-sea conoidean gastropod fauna of the Cape Point region, and Barnard's work still remains the primary reference. The Cape Point region is of particular interest due to its geographical position, because it is situated at the border between two oceans, and its deep-sea fauna may represent a mixture of Atlantic and Indo-Pacific elements.

Through the courtesy of Mrs. Michelle G. van der Merwe from the South African Museum, Cape Town (SAM), I was able to examine the type specimens of Barnard's species of deep-sea conoidean gastropods. The purpose of the present paper is to illustrate these species and to revise their taxonomic position.

In his publication, Barnard (1963) designated some specimens from his material as "types". Sometimes, when a species was represented by a few specimens, he did not mention the presence of types at all. In these cases, all such specimens are considered syntypes.

Specimens of four of Barnard's species were sent by him to the British Museum (Natural History) as "paratypes". However, the designation of paratypes without a designation of holotype is invalid. Moreover, almost all these specimens are not even syntypes, because they were not originally included into "types" (= type series) (ICZN Art. 27(b)VI).

SYSTEMATICS

Superfamily CONOIDEA Fleming, 1822

Family TURRIDAE H. & A. Adams, 1853
Subfamily TURRINAE H. & A. Adams, 1853

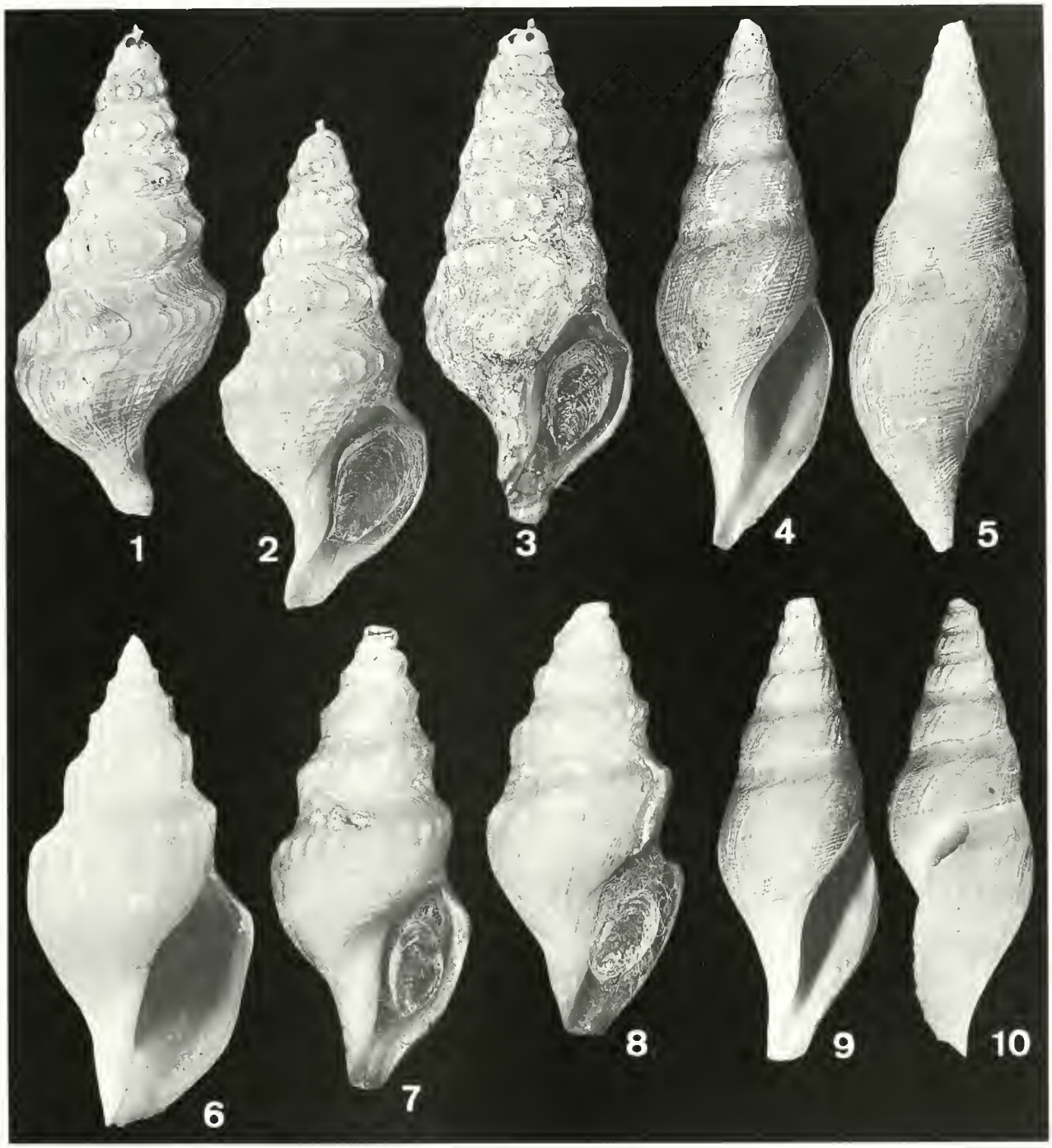
Gemmula (Ptychosyrinx) lobatopsis (Barnard, 1963)
(figures 1–3)

Turris lobata (Sowerby) [*partim*] Barnard, 1958:107, fig. 3j.
Clavatula lobatopsis Barnard, 1963:420–421, fig. 2a
Gemmula (Ptychosyrinx) lobatopsis (Barnard) Kilburn, 1983: 582.

Material examined: Three specimens (SAM A9730) indicated by Barnard (1963) as "Types".

Type locality: "Africana II", sta. A191, 33°36′S, 16°15′E, 1520–1570 fms (2780–2918 m).

Description: Two of the three syntypes are heavily corroded, though the presence of opercula indicates that they were collected alive. The best preserved specimen is here designated as lectotype (figs. 1–2). The dimensions are: lectotype—32.4 × 13.6 mm at 6.5 preserved whorls; paralectotypes—34.6 × 12.9 mm and 33.4 × 13.7 mm at 5.5 and 6+ preserved whorls, respectively. The upper whorls are eroded and partly missing in all shells. Lectotype strongly angulate at periphery. Suture slightly wavy, clear, despite Barnard's statement, visible on all whorls. Subsutural cord thin, narrow, less distinct on body whorl, with small tubercles at points of intersection with growth lines passing through peripheral gemmules. These growth lines strong, raised, especially on body whorl.



Figures 1–10. 1–3. *Gemmula (Ptychosyrinx) lobatopsis*, lectotype (**1, 2**) and paralectotype, 33.4 mm (**3**). **4–5, 9–10.** *Abyssothauma psilarosis*, lectotype (**4, 5**) and paralectotype (**9, 10**). **6.** *Gymnobela (Theta) chrysopelex*, holotype. **7, 8.** *Typhlomangelia polythele*, lectotype (**7**) and paralectotype (**8**)

Four weak, narrow, widely spaced cords between subsutural cord and row of peripheral gemmules, 3 distinct cords below gemmulate periphery on last whorls. Shell base and canal covered by 17 narrow, widely spaced cords, which gradually weaken towards the canal end. Peripheral gemmules on spire whorls mostly eroded, but preserved ones strong and acute, becoming progressively weaker, longitudinally elongate, arcuate towards the body whorl. They are numerous, irregularly placed on last half of the body whorl, almost obsolete near aperture. Penultimate whorl bears 20 gemmules, the body about 33.

Paralectotypes have less angulate whorls with less prominent peripheral gemmules. Subsutural ramp may be concave, especially on last half of the body whorl.

Siphonal canal varies in length and may be almost straight or turned to left, as in lectotype. The pattern of sculpture is not similar to that shown in Barnard's drawing (Barnard, 1963:fig. 2a), *i.e.*, with very strong and closely set bilobed tubercles forming the subsutural cord.

Remarks: This species was also recorded in the area from 33°26′S to 34°37′S and from 16°23.5′ E to 17°03′E, at 2378–3036 m (Barnard, 1963). The shells found in the John Murray Expedition, sta. 118, off Zanzibar, 1789 m, and identified as *G. teschi* (Powell, 1964) (Sysoev, in press, figs. 68–70), are *G. lobatopsis*.

Family CONIDAE Fleming, 1822

Subfamily CLATHURELLINAE H. & A. Adams, 1858

Typhlomangelia polythele Barnard, 1963
(figures 7–8)

Typhlomangelia (?) polythele Barnard, 1963:422, fig. 3e, f.

Material examined: Two syntypes (SAM A9802).

Type locality: "Africana II", sta. A317, 33°50′S, 16°30′E, 1480–1660 fms (2707–3036 m).

Description: Largest (12.3 × 5.4 mm) and better preserved of two syntypes here designated as lectotype. Its shell rather thick, consisting of 5.5 remaining whorls. Protoconch missing, first teleoconch whorl eroded. Whorls angulate at periphery. Subsutural ramp slightly concave, with narrow subsutural cord and numerous, regular, narrow, arcuate folds formed by thickened growth lines. Axial sculpture represented by numerous, very short ribs below subsutural ramp. Ribs rapidly weaken, do not reach lower suture or periphery of body whorl. Ribs number about 22 on penultimate whorl (its dorsum broken, apparently during extraction of soft body) and 26 on body. Spiral cords (7 on penultimate whorl and 32 on body whorl) are narrow, separated by wide interspaces (2–4 times wider than cords). Spiral cords are more closely set on siphonal canal. Canal short, straight. Symmetrical anal sinus occupies entire subsutural ramp, being deepest in its middle. Paralectotype (11.5 × 5.1 mm at 5+ preserved whorls) has the same conchological characters.

Remarks: Barnard provisionally placed this species in *Typhlomangelia*, which seems to be appropriate for the species, despite its small and broad shell lacking spiral sculpture on the subsutural ramp. *Typhlomangelia adenica* Sysoev, a very similar species both conchologically and in radular characters, is known from the Gulf of Aden, John Murray Expedition sta. 26 and 185, 200–2312 m (Sysoev, in press).

Abyssothauma Sysoev, 1996, new genus

Type species: *Moniliopsis psilarosis* Barnard, 1963.

Diagnosis: Shell large, to 60 mm, fusiform, with rounded and weakly convex whorls, covered by thick olivaceous periostracum. Spire more than 30% of shell height. Early whorls weakly angulate. Axial sculpture of numerous oblique narrow folds below shoulder in early whorls, or absent. Spiral sculpture of low, rather wide cords below subsutural ramp. Shell base weakly convex, not differentiated from canal. Aperture narrowly oval, siphonal canal wide, long. Anal sinus moderately deep, rounded, occupying the subsutural ramp, with deepest point in its middle. Operculum large, leaf-shaped, with terminal nucleus. Radular teeth hollow, long, slightly curved, not barbed, with rounded base and terminal opening of tooth cavity.

Remarks: The new genus resembles the genera *Typhlosyrinx* Thiele, 1925 and *Belaturricula* Powell, 1951. From the former genus it differs in having a stronger shell with better developed spiral sculpture, thick dark-colored periostracum, different form of axial sculpture on early whorls, and presence of operculum. This new genus differs from *Belaturricula* in having a narrower shell with stronger sculpture, pronounced siphonal canal and deep anal sinus. The new genus includes the type-species and a new species from the Tasman Sea, 3610–3688 m that will be described elsewhere. *Pontiothauma ergata* Hedley, 1916, resembles *A. psilarosis* in general shell outline, predominance of spiral sculpture, structure of radular teeth (see Egorova, 1982, figs. 63a, b), presence of operculum with terminal nucleus, but differs in having a shallow anal sinus (holotype illustrated by Dell, 1990: figs. 418–419) and very thin light-colored periostracum. The taxonomic position of *P. ergata* is uncertain, but it obviously does not belong to *Pontiothauma*, differing in the shell form, sculpture, the presence of operculum and different radular teeth indicating the placement in the Clathurellinae, not Raphitominae. Probably *P. ergata* belongs to a separate genus, closely related to *Abyssothauma*.

Abyssothauma psilarosis (Barnard, 1963)
(figures 4–5, 9–10)

Moniliopsis psilarosis Barnard, 1963:421–422, fig. 4a.

Material examined: Two specimens (SAM A9789) indicated by Barnard (1963) as "Types".

Type locality: Barnard (1963) did not designate the type locality nor indicate which of his two samples contained "types". However, judging from the indicated number and quality of specimens from "Africana II" sta. A316, 34°42′S, 16°54′E, 1725–1780 fms (3155–3255 m), corresponding to specimens from the type series, the type locality is restricted to these coordinates.

Description: Largest of two type specimens is here designated as lectotype. Dimensions: 47.2 × 16.0 at 6.5 preserved whorls (lectotype) and 40.8 × 14.4 at 6 preserved whorls (paralectotype). Lectotype shell strong, solid, covered by thick dark-olivaceous periostracum. Protoconch and at least one teleoconch whorl missing. Upper whorls distinctly angulate above periphery, angulation weakening in subsequent whorls, becoming obsolete in penultimate whorl. Subsutural ramp weakly

concave. Upper whorls with strong, oblique axial ribs below subsutural ramp (18 ribs on first well-preserved whorl). Ribs form small knobs in upper part. Ribs markedly weaken towards lower suture, becoming shorter in successive whorls. Last 3.5 whorls devoid of axial sculpture except for indistinct, irregular folds formed by growth lines. Spiral sculpture of initial whorls consists of wide, very low cords separated by narrow grooves. Cords become stronger and more widely spaced on two last whorls, but interspaces do not exceed cord width. Subsutural ramp lacks spiral sculpture except of 3–4 feeble striae on lower part. Aperture narrow, inner lip evenly curved, covered by a smooth callus. Siphonal canal moderately long, narrow. Paralectotype smaller, with only 2.5 whorls, lacking axial ribs. Spiral cords slightly weaker than those of lectotype. Outer lip intact, evenly projecting forward below anal sinus. Sinus rounded, moderately deep, slightly asymmetrical, with its deepest point just above middle of subsutural ramp.

Remarks: Barnard (1963) placed his species in *Moniliopsis* Conrad, 1865. However, this Eocene genus containing few species from southern USA and Peru, is characterized by a strong sculpture of very wide spiral cords cut into subrectangular nodes that are present on the subsutural ramp. In Barnard's time, *Moniliopsis* was used to include some Recent West American species which are now included in the genus *Ophiodermella* Bartsch, 1944. This genus, in turn, cannot accomodate the Barnard's species either, because it is characterized by a much lower position and different type of anal sinus.

Subfamily RAPHITOMINAE Bellardi, 1875

Gymnobela glaucocreas (Barnard, 1963)
(figures 15, 19)

Cythara (?) glaucocreas Barnard, 1963:422–423, fig. 2d

Material examined: One specimen (SAM A9821) indicated by Barnard (1963) as "Type" (holotype).

Type locality: "Africana II", sta. A318, 33°52'S, 16°51'E, 1380–1520 fms (2524–2780 m).

Description: Shell 26.0 × 11.8 mm, with 7.5 preserved whorls, greyish-white, covered by thin periostracum. Protoconch whorls eroded, probably partly missing. Early teleoconch whorls with only a slight angulation at periphery. Towards body whorl, whorls become more angulate, subsutural ramp becomes concave. Sutures shallowly channeled. Axial ribs begin in lower part of subsutural ramp, numerous (27 on body and penultimate whorls), narrow, oblique, with sharp crests. Two ribs may rarely merge together near whorl shoulder. Subsutural ramp covered by thin arcuate folds following traces of anal sinus. Folds are not always continuations of axial ribs, and are more numerous than latter (41 on body whorl, plus several similar short folds that do not reach lower part of subsutural ramp). Spiral sculpture of narrow, flattened, widely spaced cords covering entire shell surface. Cords on subsutural ramp more closely spaced. Interspaces between cords bear thinner secondary thread.

Remarks: This species has all the characteristics of *Gymnobela* Verrill, 1884. It is most similar to the North Atlantic *G. engonia* Verrill, 1884 (type species of the genus) and differs from the latter mainly in having less angulate whorls, less oblique axial ribs, and fainter spiral sculpture. The radula of *G. glaucocreas*, described by Barnard as similar to that of *G. verecunda* (Barnard, 1963), also has much in common with that of *G. engonia* (see Bouchet & Warén, 1980, fig. 26).

Gymnobela dagama (Barnard, 1963)
(figures 11–14)

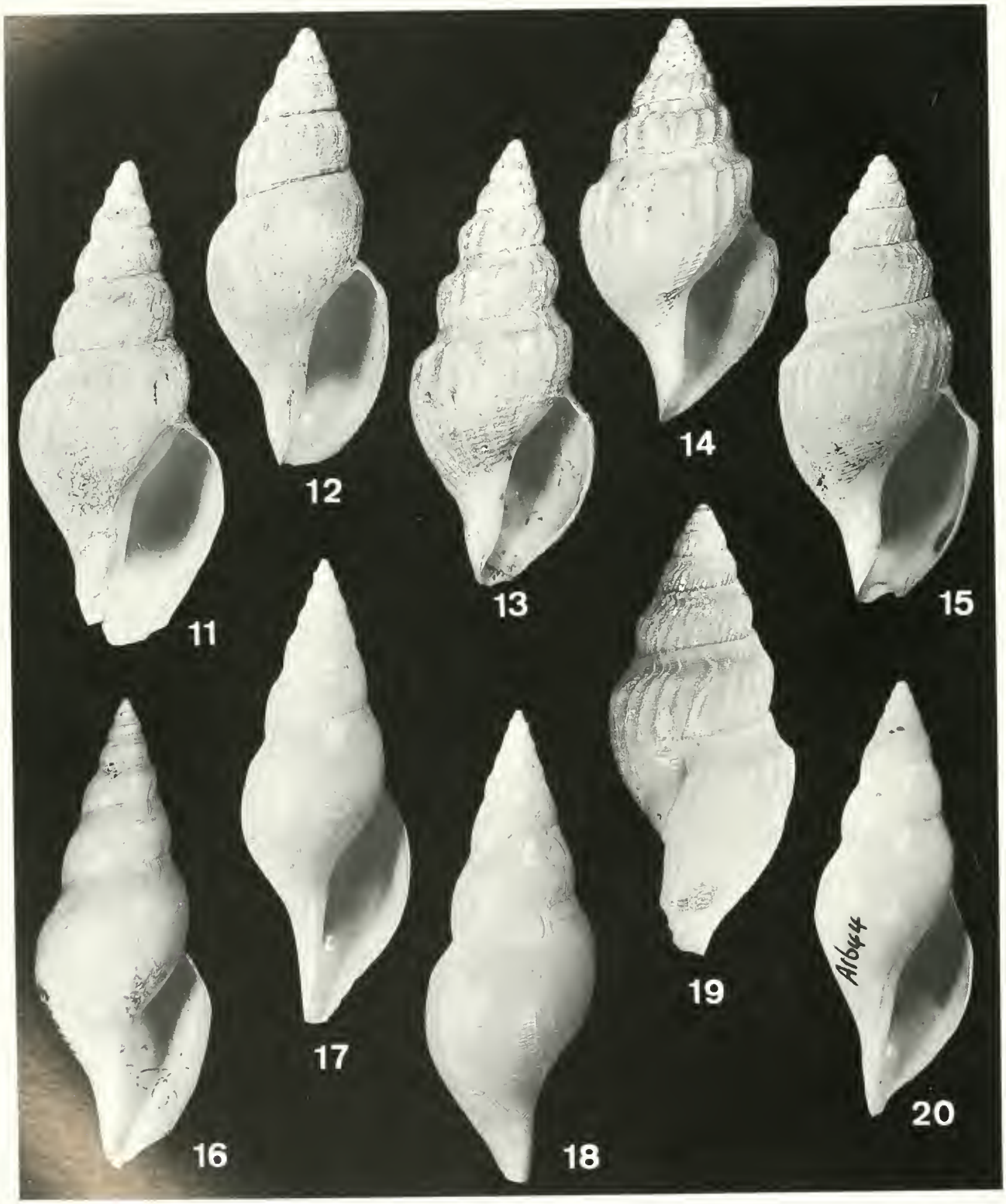
Cythara (?) dagama Barnard, 1963:423, fig. 2g, h.

Material examined: Four specimens (SAM A9731) out of 5 indicated by Barnard as "Types".

Type locality: "Africana II", sta. A191, 33°36'S, 16°15'E, 1520–1570 fms (2780–2871 m).

Description: Largest syntype (38.4 × 16.3 mm) with heavily eroded surface. Second largest specimen (32.8 × 13.8 mm) with well preserved shell (fig. 12) is here designated as lectotype. Shell of 6.5 whorls. Protoconch missing, upper whorls eroded. Sutures deeply channeled. Whorls almost evenly convex, with only slight angulation at about 1/4 of whorl height. Subsutural ramp narrow, slightly concave. Axial ribs weak, narrow, with rounded or flattened crests, numerous (19 on penultimate whorl and 27 on body whorl) and somewhat irregular in strength, especially on body whorl. Ribs begin at border of subsutural ramp and extend to lower shell base. Subsutural ramp devoid of sculpture. Spiral sculpture on spire whorls appears to consist of wide, flattened cords separated by narrow grooves due to the erosion of surface. Cords well preserved and are narrow and widely spaced (interspaces 1.5–2 times wider than cord) only in some shell areas, particularly on body whorl. Aperture oval, with short, wide siphonal canal poorly differentiated from aperture. Judging from growth lines, outer lip very slightly projects forward below anal sinus. Anal sinus narrow, with its deepest point at middle of subsutural ramp. Two smaller paralectotypes (31.3 × 13.1 mm and 23.6 × 11.5 mm at 7+ and 6+ whorls, respectively) have more angulate whorls with more concave subsutural ramp, especially in smallest, best preserved specimen. This specimen has weak spiral cords on lower part of subsutural ramp, covered by numerous thin arcuate folds formed by thickened growth lines.

Remarks: The radula (Barnard, 1963, fig. 2h) is not characteristic of *Gymnobela* and more closely resembles that of *Benthomangelia* Thiele, 1925. However, the conchological characters indicate the assignment of this species to *Gymnobela*. Besides the type locality, the species was found in the area from 33°36' to 34°37'S and from 16°15' to 17°03'E, at 2707–3219 m (Barnard, 1963).



Figures 11–20. 11–14. *Gymnobela dagama*, lectotype (**12**) and paralectotypes (**11, 13, 14**; 38.4, 31.3, and 23.6 mm, respectively). **15, 19.** *Gymnobela glaucocreas*, holotype. **16–18, 20.** *Xanthodaphne pyrropelex*, lectotype (**17–18**) and paralectotypes (**16, 20**; 49.3 and 44.7 mm, respectively).

Gymnobela verecunda (Barnard, 1963)
(figures 21–24)

Daphnella (?) verecunda Barnard, 1963:427–428, fig. 2e.

Material examined: Three syntypes (SAM A9697).

Type locality: "Africana II", sta. A189, 33°50'S, 17°21'E, 600 fms (1097 m).

Description: Largest (shell 22.4 × 10.8 mm) of three syntypes best preserved, and here designated as lectotype (figs. 21–22). Shell white, consisting of 7 preserved whorls (uppermost broken). Protoconch missing. Spire whorls angulate at periphery, subsutural ramp slightly concave. Axial ribs begin in lower part of subsutural ramp, very rapidly become prominent at shoulder, and gradually weaken below, not reaching canal. Ribs strong, oblique, narrow, 15 ribs on penultimate whorl, 16 on body whorl. Some growth lines on subsutural ramp thickened near upper suture. Spiral sculpture on subsutural ramp consisting of weak, narrow threads, which appear at some distance from upper suture and become stronger towards shoulder. Spiral sculpture on subsutural ramp not always visible due to shell erosion. Spiral cords below the shoulder rather wide, flattened, sometimes with a narrower secondary cord in interspaces. Siphonal canal short, slightly twisted. Anal sinus, judging from growth lines, is asymmetrical, with its deepest point in lower half of subsutural ramp. Paralectotypes are 19.5 × 9.5 and 16.6 × 8.3 mm in size. Larger paralectotype better preserved, with 15 axial ribs on body whorl and wider spiral cords than in lectotype. All three shells have a characteristic light-orange staining on columella.

Remarks: Besides the type locality, the species was also found off northern Namibia (19°45'S), at 1600 m, R/V "Professor Shtokman", sta. 1563 (Sysoev, unpublished data).

Gymnobela (Theta) chrysopelex (Barnard, 1963)
(figure 6)

Typhlosyrinx chrysopelex Barnard, 1963:425, fig. 3g, h.

Material examined: One specimen (SAM A9857) (holotype).

Type locality: "Africana II", sta. A322, 34°36'S, 17°00'E, 1500–1760 fms (2743–3219 m).

Description: Shell 18.8 × 8.6 mm, white, with glossy surface. Protoconch of three preserved whorls (at least 1–1.5 initial whorls missing), diameter 1.25 mm. Protoconch sculpture not well preserved, consisting of arcuate axial riblets passing from suture to suture. Riblets on lower half of whorl diagonally crossed by oblique riblets beginning at lower suture. Teleoconch of 4.75 whorls. First whorl angulate slightly above periphery, penultimate whorl at about 1/3 of whorl height. Oblique axial ribs beginning just above whorl angulation, slightly weaken below, and reaching lower suture and upper shell base. Ribs 15 on penultimate whorl, 18 on body whorl. Spiral sculpture of obscure striations below whorl angulation, feeble threads on lower part of shell base and canal. Based on growth lines, anal sinus very shallow as compared to congeners.

Remarks: This species agrees well with the subgenus *Theta* Clarke, 1959 in the shell outline and sculpture. The protoconch is very similar to that of *G. (T.) chariessa* (Watson, 1881) (see Bouchet & Warén, 1980: figs. 254, 255), but larger than in that species. The radular teeth (Barnard, 1963, fig. 3h) are typical of *Gymnobela*. *Gymnobela (T.) chrysopelex* is closely related to *G. (T.) chariessa*, but differs in having a shallower anal sinus, larger protoconch, and less oblique axial ribs.

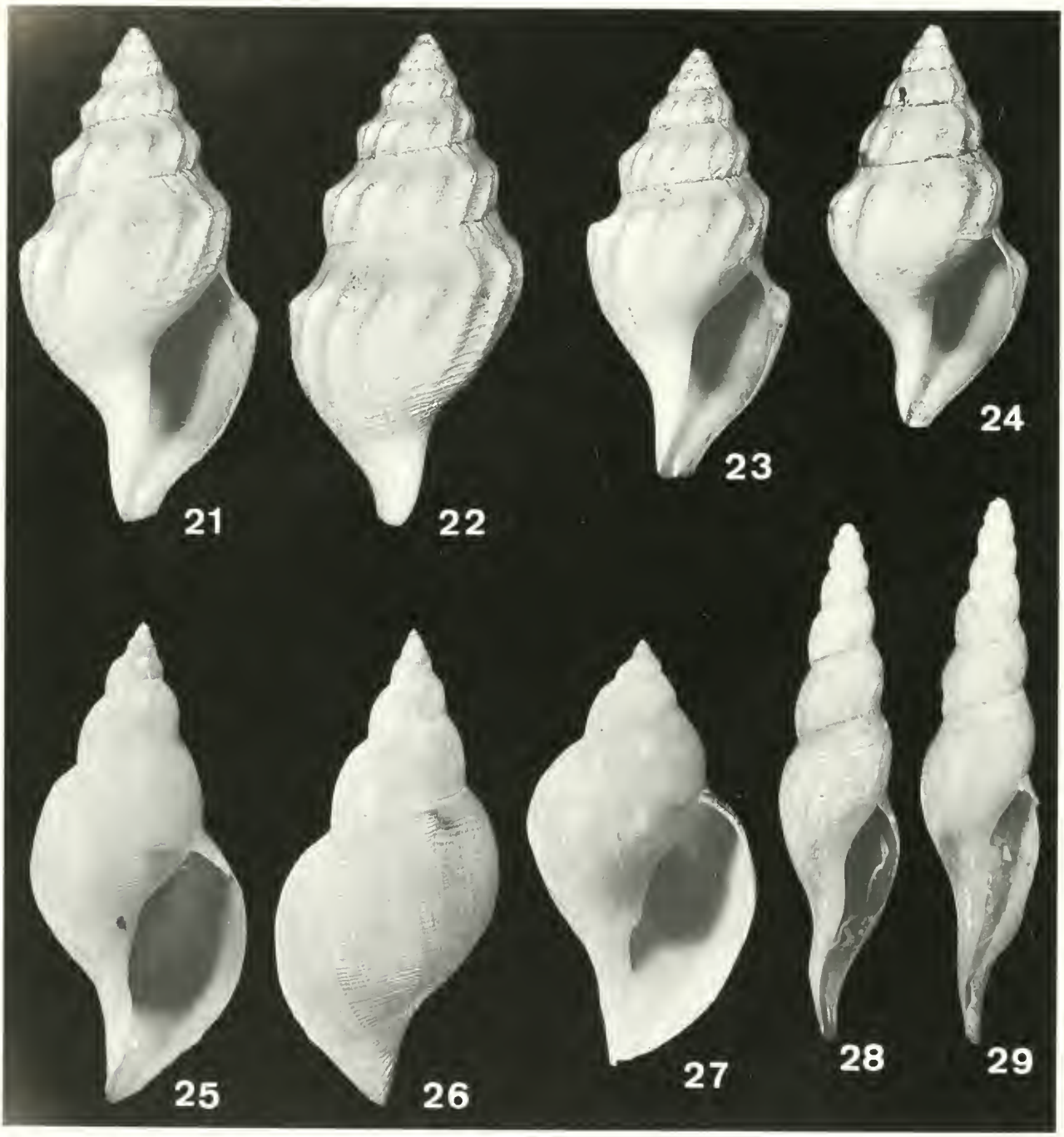
Xanthodaphne pyrropelex (Barnard, 1963)
(figures 16–18, 20)

Pleurotoma (Surcula) dissimilis (*non* Watson)—Barnard, 1958: 147–148, fig. 23a.
Typhlosyrinx pyrropelex Barnard, 1963:423–425, fig. 2c.

Material examined: Four specimens (SAM A1643, SAM A1644, SAM A1645) out of 5 indicated by Barnard (1963) as "Types".

Type locality: Barnard did not designate the type locality, and the type series came from three different localities described as "Cape Point N. 77°E. 650–700 fathoms; NE. × E. 1/2 E. 43 miles, 900 fathoms; NE. × E 3/4 E. 38 miles, 750–800 fathoms". The syntypes were collected by the Cape Goverment trawler s.s. "Pieter Faure", but the respective station numbers were not indicated in the publications (Barnard, 1958, 1963) or on labels. Assuming that Barnard (1963: 424) listed localities and museum numbers in the same order, the lectotype was found in the second of above-mentioned localities.

Description: Largest syntype (SAM A1643, 49.3 × 18.5 mm at 7 teleoconch, 1.5 preserved protoconch whorls) with slightly broken canal, eroded parts of body whorl. Another syntype (SAM A1645, 45.0 × 15.3 mm) strongly eroded, with broken aperture. Largest of two remaining syntypes designated here as lectotype (figs. 17–18). Shell 48.2 × 17.2 mm, white, thin, fragile. Protoconch of 1.5 preserved brown whorls with thin oblique arcuate axial riblets. Ribs more crowded and irregular near the transition to teleoconch, less inclined, occasionally bifurcating in lower part. Teleoconch whorls (6.8 in number) almost evenly rounded, with well-marked subsutural ramp, slightly concave in early whorls, almost flat in last ones. Border of subsutural ramp defined by shallow groove. Some growth lines on subsutural ramp thickened below suture, which is more pronounced in early whorls. Subsutural ramp devoid of spiral sculpture except for indistinct striation on its lower part. Spiral sculpture below shoulder consisting of very low, flattened, wide, slightly wavy cords with serrated edges, separated by narrow grooves. Cords becoming stronger, narrower below body whorl periphery. Based on growth lines, the



Figures 21–29. 21–24. *Gymnobela verecunda*, lectotype (**21–22**) and paralectotypes (**23, 24**; 19.5 and 16.6 mm, respectively). **25–27.** *Xanthodaphne subrosea*, lectotype (**25–26**) and paralectotype (**27**). **28–29.** *Famelica hitrudis*, lectotype (**28**) and paralectotype (**29**).

anal sinus subsutural, wide, deep. Its margin almost vertical below suture, nearly horizontal at border of subsutural ramp. Outer lip very strongly projecting forward below sinus. Paralectotypes very similar to lectotype, varying insignificantly in details of spiral sculpture. None have more intact protoconch than on lectotype.

Remarks: The species has all the essential characters of *Xanthodaphne* Powell, 1942. Protoconch sculpture is similar to that of the type species of the genus, *Pleurotoma membranacea* Watson, 1886. However, the shell of *X. pyrropelex* is more slender than that of most other representatives of the genus. *Xanthodaphne pyrropelex*

species was also recorded in the area from 33°36′S to 34°36′S and from 16°15′E to 17°00′E, at 2524–3219 m (Barnard, 1963).

Xanthodaphne subrosea (Barnard, 1963)
(figures 25–27)

Typhlosyrinx subrosea Barnard, 1963:425–426 , fig.3a-d

Material examined: Two syntypes (SAM A9822).

Type locality: "Africana II", sta. A318, 33°52′S, 16°51′E, 1380–1520 fms (2524–2780 m).

Description: Larger of two syntypes (36.0 × 16.2 mm) designated here as lectotype. Shell white, semi-transparent, fragile. Protoconch of at least 3.5 brown whorls (upper whorls eroded) sculptured by numerous arcuate axial riblets on upper half, diagonally cancellated on lower half. Protoconch diameter 1.45 mm. Teleoconch of 4.75 evenly convex, rapidly expanding whorls. Whorls smooth initially, then obscure spiral striations appear, turning into rather strong and flattened cords (about 60 on body whorl) covering the entire whorl except for narrow area just below upper suture. Strongest, most widely spaced cords situated on whorl shoulder. These cords appear first on shell. Interspaces between cords usually do not exceed the cord width at whorl periphery. Siphonal canal rather long, slightly twisted. Inner lip without callus. Based on growth lines, anal sinus subsutural, outer lip greatly projecting forward below sinus. Paralectotype with much smaller, proportionally broader shell (20.3 × 11.0 mm), its protoconch consisting of about 4.5 whorls. Upper whorls eroded, others with sculpture similar to that of lectotype. Protoconch diameter 1.35 mm. Spiral sculpture similar to that of respective whorls of lectotype. Sculpture irregular on most of body whorl, due to scar of heavy damage to shell. Inner lip covered by very thin callus.

Remarks: The species corresponds well to the diagnosis of *Xanthodaphne*, and is quite similar to its type-species, *X. membranacea*. The only difference is that the protoconch sculpture in *X. membranacea* is mainly axial. However, the protoconch sculpture of *X. subrosea* falls within the range of variability characteristic of the genus in general (see Bouchet & Warén, 1980: figs. 234–237).

Famelica bitrudis (Barnard, 1963)
(figures 28–29)

Daphnella (?) bitrudis Barnard, 1963: 428, fig. 1b.

Material examined: Two syntypes (SAM A9754).

Type locality: "Africana II", sta. A193, 33°49′S, 16°30′E, 1500 fms (2743 m).

Description: Larger syntype (15.2 × 3.4 mm) with broken aperture, partly broken penultimate whorl. Smaller syntype (13.6 × 3.3 mm) here designated as lectotype. Shell very narrow, semi-transparent, white, very fragile, consisting of 7.5 whorls, uppermost whorl(s) missing. Upper 3 whorls with eroded surface, differing in their proportions from subsequent whorls, apparently representing a protoconch. Teleoconch whorls rather evenly convex, with clearly defined subsutural ramp, bordered by spiral cord corresponding to lower, almost horizontal branch of anal sinus. Spiral sculpture developed below subsutural ramp, consisting of weak narrow cords separated by wide (2–3 times wider than cords) interspaces. Cords weaken on shell base, with smooth band at transition of shell base to canal. Sculpture resuming on canal, but with very weak cords. Siphonal canal long, narrow, twisted. Anal sinus subsutural, not very broad. Outer lip projects forward below anal sinus. Paralectotype differs only in having slightly more numerous and more closely spaced spiral cords (12 on the penultimate whorl vs. 11 in the lectotype).

Remarks: In their original description of *Famelica*, Bouchet and Warén (1980), the authors included *Daphnella bitrudis* in their new genus.

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Systematic Relationships Among Florida Populations of *Argopecten irradians* (Lamarck, 1819) (Bivalvia: Pectinidae)

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ABSTRACT

Morphometric and genetic examinations (using allozyme electrophoresis) were conducted on two Florida populations of bay scallops, *Argopecten irradians* (Lamarck, 1819), to investigate the status of the subspecies *A. i. taylorae* Petuch, 1987. One other Florida population [*A. i. concentricus* (Say, 1822)] was examined morphometrically. Morphometric examinations emphasized mensural and meristic characters used in previous systematic diagnoses. Morphometric data were analyzed using analysis of variance and principal component analysis. Scallops taken from Florida Bay (putatively *A. i. taylorae* Petuch, 1987) were smaller but otherwise not morphologically distinct from populations of *A. i. concentricus* (Say, 1822) from Pine Island Sound and Homosassa Bay, Florida. Mean Nei's modified genetic distance value shows a close relationship between Florida Bay and Homosassa Bay scallops. Neither morphometric nor genetic evidence supports the proposed status of *A. i. taylorae* as distinct from Florida populations of *A. i. concentricus*.

Key words: Pectinidae, *Argopecten irradians*, morphometrics, systematics.

INTRODUCTION

Scallops are often distributed in patchy or contagious patterns, and, although disjunct local populations may be joined by variable degrees of larval exchange to form metapopulations (Levins, 1970; Andrewartha & Birch, 1984; Roughgarden *et al.*, 1985; Roughgarden & Iwasa, 1986; Simberloff, 1988; Hanski, 1989; Orensanz *et al.*, 1991), local populations along a species' range are probably self-sustaining (Sinclair *et al.*, 1985). Expectedly, reproductive isolation may contribute to genetic drift that can produce locally distinctive morphologies. The bay scallop, *Argopecten irradians* (Lamarck, 1819), which inhabits semi-enclosed coastal bays, sounds, and estuaries from Cape Cod, Massachusetts, to Tampico, Mexico (Clarke, 1965; Abbott, 1974), exemplifies the results of such isolation (Clarke, 1965; Waller, 1969; Kraeuter *et al.*, 1984).

Three extant subspecies of *A. irradians* have customarily been recognized: *Argopecten irradians irradians* (Lamarck, 1819), distributed from Cape Cod to New Jersey; *A. i. concentricus* (Say, 1822), distributed from New Jersey to South Carolina and from Palm Beach Inlet, Florida, to Louisiana; and *A. i. amplicostatus* (Dall, 1898), distributed from Texas into Mexico (Clarke, 1965; Waller, 1969, 1991; Abbott, 1974). A fourth subspecies, *A. i. sablensis* (Clarke, 1965), described from shells collected in Nova Scotia, apparently became extinct during the Holocene (Waller, 1969). These subspecies have been distinguished morphologically by plical number and shape, valve size and shape, and valve coloration (Clarke, 1965; Waller, 1969; Abbott, 1974). Bricelj *et al.* (1987), however, cautioned that subspecific distinctions within *A. irradians* have not yet been substantiated by biochemical techniques.

Recently Petuch (1987) described an additional subspecies of bay scallop, *Argopecten irradians taylorae*, based upon specimens from Rabbit Key Basin, Florida, and reported it to be restricted to Florida Bay and the western sides of the middle and upper Florida Keys (figure 1). Petuch (1987) reported that plicae of *A. i. taylorae* were more numerous than those of the other subspecies and that plicae were lower, wider, and more flattened than in *A. i. concentricus*. The valves of *A. i. taylorae* were also said to be much smaller, more fragile, and much more colorful than those of *A. i. concentricus* (table 1).

To emphasize the geographic isolation of *Argopecten irradians taylorae*, Petuch (1987) gave the distributional

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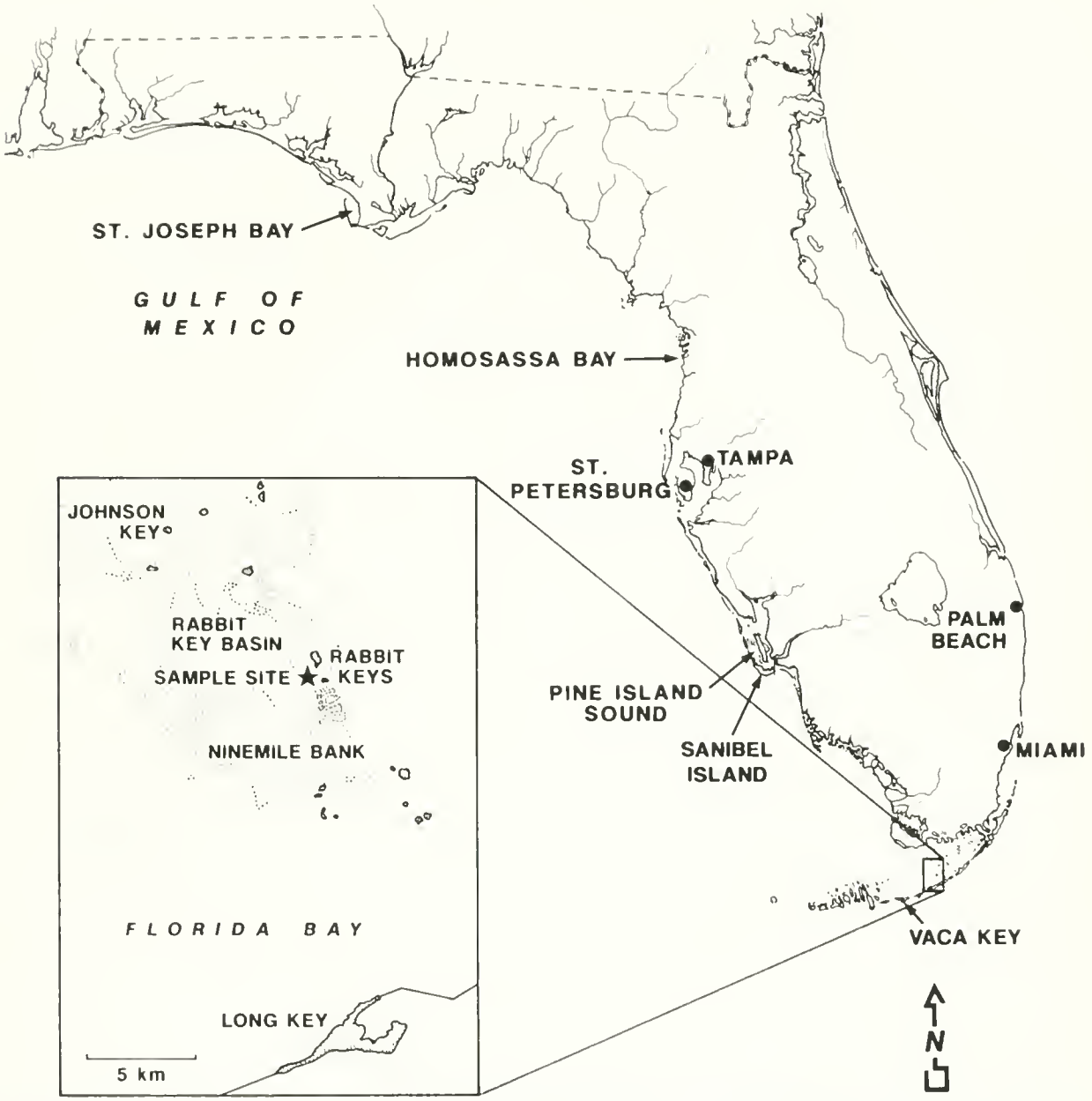


Figure 1. Florida collecting locations of *Argopecten irradians* populations used in analyses and additional localities relevant to bay scallop populations. Inset shows location of collection within Rabbit Key Basin.

range of *A. i. concentricus* as "New Jersey to Georgia, and. . .Tampa, Florida to Louisiana." In doing so, he overlooked earlier Florida records of bay scallops at Boca Grande and Sanibel Island (Clarke, 1965); at Whitewater Bay, Sandy Key Basin, and south of Flamingo in Florida Bay (Tabb & Manning, 1961); and at several locations from Vaca Key in the middle Keys northward through Biscayne Bay to Palm Beach Inlet on the Florida east coast (Waller, 1969). Clarke (1965) and Waller (1969) had previously reported specimens from all of these locations as *A. i. concentricus*, but at least some of the specimens came from within the range of *A. i. taylorae*.

An investigation of the systematic status of *Argopecten irradians taylorae* was prompted by the need to address resource management issues. Bay scallops have historically supported small-scale commercial fisheries at various locations between Pensacola Bay and Pine Island Sound along Florida's west coast. Although the commercial fishery has decreased substantially in recent years, the species continues to be the target of an important recreational fishery throughout much of that region (Arnold, 1990). The presence of an isolated subspecies of bay scallop in Florida Bay, as reported by Petuch (1987), could have ramifications for resource management. The

Table 1. Characters of subspecies of *Argopecten irradians* reported by previous authors.

Subspecies	Clarke, 1965	Waller, 1969	Abbott, 1974	Petuch, 1987
Argopecten irradians irradians	16–20 (usually 16–18 ribs; ribs rounded, valve length and height nearly equal, L/H ratio approx. 1.06; W/H ratio approx. 0.21 (left) and 0.24 (right); right valve color as in Abbott (1974) but commonly white (or nearly so).	15–20 ribs; ribs low and rounded; L ≈ H; valves thinner and flatter and ribs lower than *A. i. concentricus*.	17–18 ribs; ribs low and roundish; valves most compressed of the 3 subspecies; right valve color only slightly lighter than left.	
Argopecten irradians concentricus	17–23 ribs; ribs rounded or with flattened tops; L/H ratio approx. 1.03 (l) and 1.02 (r); valves somewhat inflated, W/H ratio approx. 0.26 (l) and 0.32 (r); 75–100% of specimens with white or nearly white right valves, color otherwise like left valve except lighter.	15–22 ribs; ribs high, sharply rounded, becoming semi-hexagonal distally; differs from *A. i. irradians* by having thicker and more convex valves and higher ribs; differs from *A. i. amplicostatus* by having thinner and less convex valves.	19–21 ribs; ribs squarish; right valve much more convex than left; right valve lightest in color of the subspecies, commonly all white.	
Argopecten irradians amplicostatus	12–18 (usually 14–16) ribs; ribs rounded to slightly flattened; L/H ratio approx. 1.0 (l) and 1.01 (r); shell more inflated than other 2 subspecies, W/H ratio approx. 0.29 (l) and 0.34 (r); color of right valves usually white, sometimes with slight color tinge.	13–17 ribs; ribs high, sharply rounded proximally, becoming low and trapezoidal to semi-hexagonal distally; differs from *A. i. concentricus* by having thicker, more convex valves with fewer ribs.	12–17 ribs; right valve with high, squarish ribs; shell more gibbose than other subspecies; right valve commonly white.	
Argopecten irradians taylorae				23–25 ribs; ribs flatter and wider when compared with *A. i. concentricus*; shell smaller, more fragile and more colorful than *A. i. concentricus*; right valve generally yellow rather than white, with more brown mottlings than *A. i. concentricus*.

population might require separate management because of the increasingly popular recreational fishery or might require protection as a rare and isolated subspecies.

We used both allozyme electrophoresis and morphometric analyses to investigate the relationship of the Florida Bay population of *Argopecten irradians taylorae* to the Homosassa Bay population of *A. i. concentricus*. Valve characters were analyzed morphometrically for two Florida populations of *A. i. concentricus* and one of *A. i. taylorae*, as well as for the type series of *A. i. taylorae*.

Although subspecific morphometric variation within *A. irradians* has been investigated in other studies (Clarke, 1965; Waller, 1969), no effort had been made to characterize corresponding genetic variation. This study is the first to examine both morphological and genetic variation within a putative subspecies of *Argopecten irradians*.

MATERIALS AND METHODS

Bay scallops (n = 66) were collected from Rabbit Key Basin, the type locality of *Argopecten irradians taylorae*, on 29 August 1990. The scallops were located in the southeastern portion of the basin, in a turtle grass (*Thalassia testudinum* Banks ex König) bed, at a depth of approximately 2 m. At that time we also collected empty valves (n of right valves = 13) of *A. i. taylorae* from that locality. Scallops were returned to the Florida Department of Environmental Protection's Keys Marine Laboratory on Long Key, where sections of adductor muscle and mantle tissue were dissected from live animals and stored in liquid nitrogen for subsequent genetic analysis. Shells were disarticulated, numbered, and returned to the Florida Marine Research Institute at St. Petersburg. Additional samples of bay scallops were collected from Homosassa Bay (n = 60), just west of the mouth of the Homosassa River, on 24 July 1990 and from Pine Island Sound (n = 56) on 28 June 1991. The specimens from Homosassa Bay and Pine Island Sound were also collected from shallow ($z \leq 2$ m) *T. testudinum* beds; Homosassa Bay scallops were also examined both genetically and morphometrically, but Pine Island Sound scallops were examined only morphometrically.

Electrophoresis. Tissue samples of scallops from Homosassa Bay and Rabbit Key Basin were analyzed for genetic composition using methods reported in Bricelj and Krause (1992). Eight polymorphic loci (frequency of the most common allele ≤ 0.99) were examined, representing the following enzymes: phosphoglucomutase (PGM, EC 2.7.5.1), glucose-6-phosphate isomerase (GPI, EC 5.3.1.9), octopine dehydrogenase (ODH, EC 1.5.1.11), superoxide dismutase (SOD-1, EC 1.15.1.1), α-amino acyl peptide hydrolase (LAP, EC 3.4.1.-), alanyl aminopeptidase (AAP, EC 3.4.1.-), dihydrolipoamide dehydrogenase (DHLD, EC 1.8.1.4), and nonspecific aminopeptidase (AP, EC 3.4.1.-). SOD-1 was only weakly polymorphic (three alleles, $\bar{H} = 0.03$), and DHLD was inconsistently resolved; thus these two loci were not included in the data analysis.

The following enzymes examined were monomorphic: superoxide dismutase (SOD-2), β-galactosidase (β-GAL, EC 3.2.1.23), isocitrate dehydrogenase (two loci, IDH-1 and IDH-2, EC 1.1.1.42), mannose phosphate isomerase (MPI, EC 5.3.1.8), 6-phosphogluconate dehydrogenase (PGD, EC 1.1.1.44), catalase (CAT, EC 1.11.1.6), glycerol-3-phosphate dehydrogenase (GPDH, EC 1.1.1.8), triose phosphate isomerase (TPI, EC 5.3.1.1), esterase (two isozymes, EST-1 and EST-2, EC 3.1.-.-), arginine kinase (ARK, EC 2.7.3.3), L-iditol dehydrogenase (IDDH, EC 1.1.1.14), and malic dehydrogenase isozymes (MDH-1 and MDH-2, EC 1.1.1.37).

Alleles were designated using standard notation: the most common allele at each locus was assigned a value of 100 and other alleles were defined based on mobility relative to the most common allele.

Observed genotypic frequencies were compared with those expected under Hardy-Weinberg equilibrium using the *G*-test and, when necessary, Williams' correction for small sample size (Sokal & Rohlf, 1981). Rare alleles were pooled with the electrophoretically closest common allele to obtain genotypic class frequencies >5. Heterozygote deficit or excess was determined from the D statistic where D is the percentage deficit (Selander, 1970); negative D values indicate a deficit of heterozygous genotypes. Allele frequencies among populations were compared using the R × C test of independence and the *G*-test (Sokal & Rohlf, 1981). Nei's modified genetic distance (Nei, 1978) was calculated for each population pair surveyed.

Morphometrics. Morphological characters of scallops in populations from Homosassa Bay, Pine Island Sound, and Rabbit Key Basin and of the holotype (USNM 859901) and paratypes (USNM 859902) of *Argopecten irradians taylorae* were examined following the methods of Waller (1969). We also collected and examined a sample of recently emptied valves of scallops (putatively *A. i. taylorae*) from Rabbit Key Basin that appeared morphologically identical to living scallops from that area. For each scallop we counted right valve plicae and measured plical height, plical width, and 13 other valve characters dimension that have been applied in morphological comparisons of bay scallops (Clarke, 1965; Waller, 1969; Abbott, 1974; Petuch, 1987) (Appendix 1).

Mensural characters used by Petuch (1987) in his diagnosis were examined using analysis of variance (ANOVA) for their relationship to valve size in the same four populations. Data from the type series of *A. i. taylorae* from Rabbit Key Basin were deleted from the analyses of population effects because of the small sample size (n = 9) and the resultant undue influence on the statistical models.

Principal component analysis (PCA) was performed using only mensural variables. Marcus (1990) suggested that measurement error can unduly influence variability in the PCA model, so standard errors of measurement were calculated for each mensural character to estimate measurement error. Each character was measured 10 times on each of six specimens, two from each population, and standard errors were calculated for each specimen-by-character combination. Standard errors were then expressed as a percentage of the mean. Using all fifteen variables we log transformed ($\log_{10}$) the values and performed a standard PCA (PRINCOMP procedure, SAS Institute, Inc., 1985). Burnaby's (1966) method of size-corrected PCA was performed separately on all data [size-corrected PCA (N. Macleod, personal communication)]. Burnaby's method removes most of the influence of size on the PCA by constructing variables orthogonal

Table 2. Allele frequencies for polymorphic enzymes from populations of *Argopecten irradians* from Rabbit Key Basin and Homosassa Bay, Florida. n = number of alleles sampled (2 × number of individuals). N_e = effective number of alleles (after Hartl & Clark, 1989).

Locus	Allele	Frequency RKB	Frequency HOM
AP	108	0	0.02
	104	0.38	0.23
	100	0.53	0.51
	96	0.08	0.24
	94	0.01	0
	n	132	118
	N_e	2.32	2.70
AAP	102	0	0.03
	100	0.35	0.40
	98	0.17	0.24
	97	0.13	0.04
	96	0.19	0.17
	94	0.15	0.13
	n	132	112
	N_e	4.37	3.79
LAP	100	0.62	0.85
	96	0.37	0.15
	94	0.01	0
	n	132	118
	N_e	1.92	1.35
ODH	106	0.01	0.02*
	104	0.08	0.13
	102	0	0.01
	100	0.77	0.80
	96	0.07	0
	94	0.01	0.04
	90	0.05	0
	n	132	118
	N_e	1.63	1.52
PGM	98	0.02	0.01*
	96	0.49	0.56
	95	0.14	0.18
	94	0.13	0.19
	92	0.11	0.01
	91	0.03	0
	90	0.07	0.05
	n	132	118
	N_e	3.36	2.61
GPI	150	0	0.01
	106	0.06	0.02
	104	0.61	0.62
	100	0.30	0.33
	99	0.02	0.01
	98	0.01	0
	n	132	118
	N_e	2.14	2.02

* Genotype frequencies not in Hardy-Weinberg equilibrium.

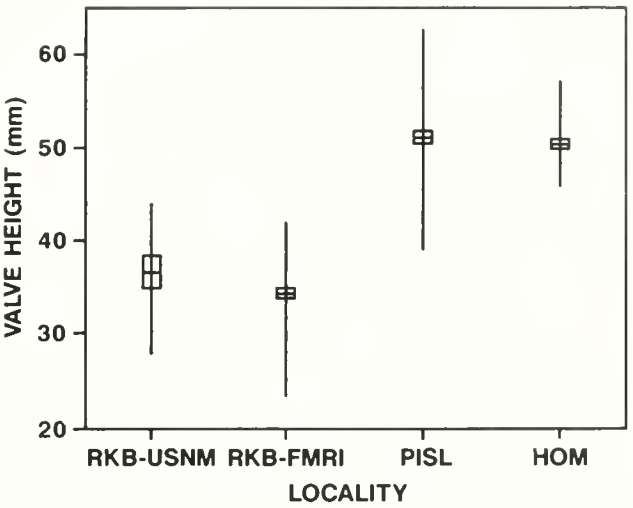


Figure 2. Valve heights of Florida Gulf coast *Argopecten irradians* populations. Plots show mean, range, and ± 1 standard error. RKB-USNM: Rabbit Key Basin, type series of *Argopecten irradians taylorae*, USNM 859901 & 859902; RKB-FMRI: Rabbit Key Basin, collection made for this study, FSBC I 41441; PISL: Pine Island Sound, FSBC I 44439; HOM: Homosassa Bay, FSBC I 40337.

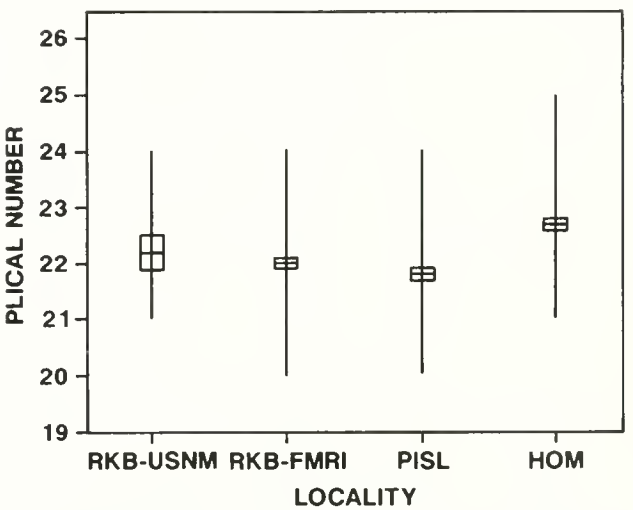
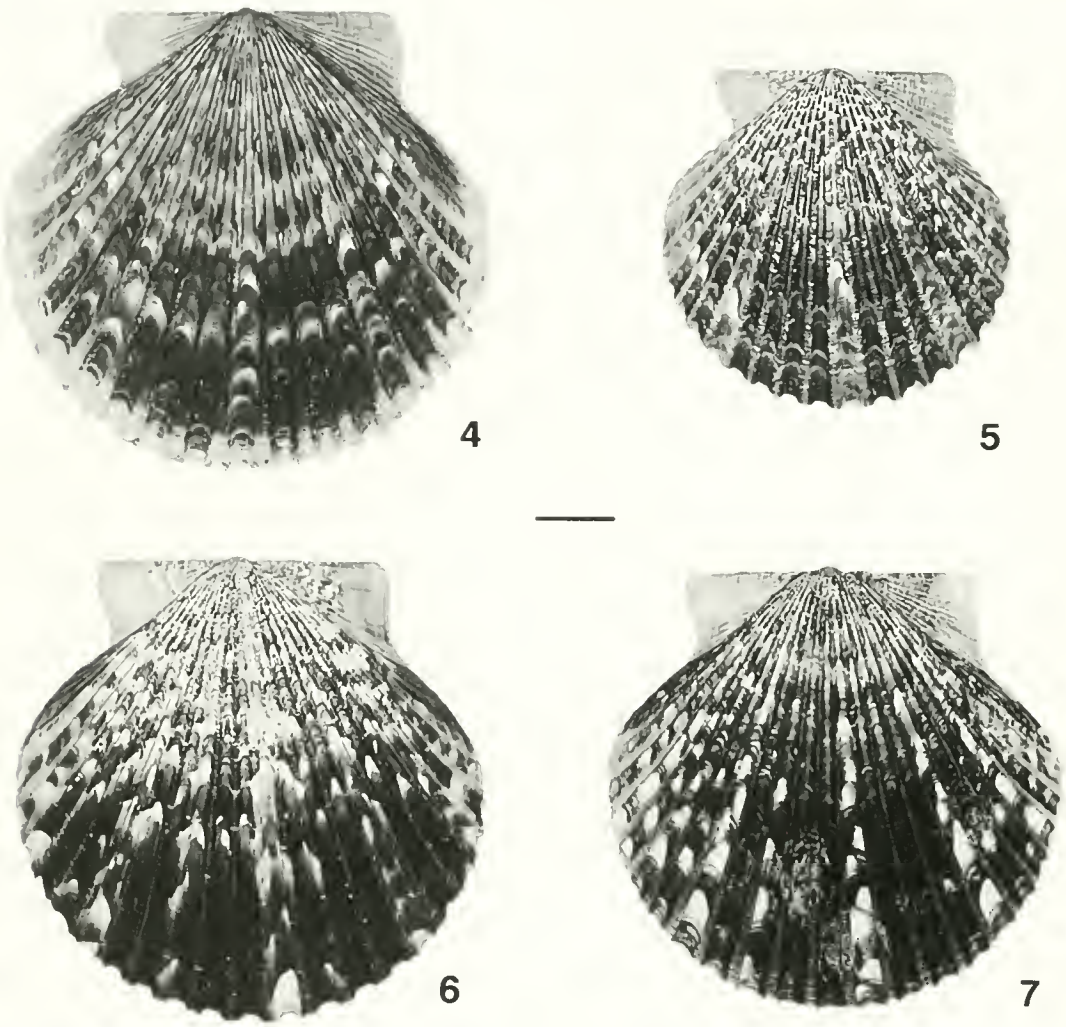


Figure 3. Numbers of right valve plicae for Florida Gulf coast *Argopecten irradians* populations. Plots show mean, range, and ± 1 standard error. RKB-USNM: Rabbit Key Basin, type series of *Argopecten irradians taylorae*, USNM 859901 & 859902; RKB-FMRI: Rabbit Key Basin, collection made for this study, FSBC I 41441; PISL: Pine Island Sound, FSBC I 44439; HOM: Homosassa Bay, FSBC I 40337.

to a variable that is considered to represent size (Rohlf & Bookstein, 1987). The relative contribution of each variable to the variation represented by PC2 and PC3 was determined, and Cattell's (1966) scree test was used to identify and eliminate variables that failed to add substantially to the variance in the analysis, leaving 9 variables: AM, AD, DG, AK, GP, BJ, IW, ad, and ce (see Appendix 1 for explanations). Using only these variables, data were reanalyzed, and size-adjusted shape variation among populations was examined using PC2 and PC3 generated by the Burnaby technique.



Figures 4–7. Left valves of *Argopecten irradians* from Florida. **4.** *A. i. concentricus*, height 60.0 mm, Rabbit Key Basin, FSBC I 41441. **5.** *A. i. taylorae*, holotype, height 44.0 mm, Rabbit Key Basin, USNM 859901. **6.** *A. i. concentricus*, height 60.1 mm, Homosassa Bay, FSBC I 40337. **7.** *A. i. concentricus*, height 57.9 mm, Pine Island Sound, FSBC I 44439. Scale bar = 10 mm.

Growth relationships of valve characters within and between populations were examined using the method of Jolicoeur (1963). Eigenvectors (coefficients) of PC1 from the standard PCAs using log-transformed data for all populations combined and separately on populations from the three localities were compared with $(1/p)^{0.5}$, where p = the number of variables and therefore $(1/p)^{0.5} = 0.333$. Coefficients for valve characters that varied above or below 0.333 represented factors that reflected positive or negative allometry.

Valve color and pattern were examined following the criteria of Elek and Adamkewicz (1990), with the exception that the relationship between color pattern and population was examined using the nonparametric Kruskal-Wallis procedure.

Disposition of specimens: Except for the type material of *Argopecten irradians taylorae*, valves of all specimens examined have been deposited in the Florida Marine Research Institute Invertebrate Collection, lot numbers FSBC I 40337 (Homosassa Bay), FSBC I 41441 (Rabbit Key Basin), and FSBC I 44439 (Pine Island Sound).

RESULTS

Electrophoresis. Among the polymorphic loci no significant differences were found between populations for the loci GPI, ODH, AAP, or PGM. Allele frequencies between Homosassa Bay and Rabbit Key Basin populations were significantly different for amino peptidase (AP, $p < 0.05$) and leucine amino peptidase (LAP, $p < 0.001$) (table 2).

The mean percentages of heterozygous loci per individual (MLH) for Homosassa Bay and Rabbit Key Basin populations were 43% and 44% using the six polymorphic loci. Homosassa Bay scallops fit Hardy-Weinberg expectations for heterozygosity at all loci, but the Rabbit Key Basin population had heterozygote deficits at the PGM ($p < 0.05$) and ODH ($p < 0.01$) loci.

Table 3. Growth relationships for valve characters from Rabbit Key Basin (RKB), Pine Island Sound (PISL), and Homosassa Bay (HOM), Florida *Argopecten irradians* populations analyzed using principal component analysis. Numbers are eigenvectors of principal component 1 and indicate positive or negative allometric growth where eigenvectors vary above or below $1/\sqrt{p}$, where p = the total number of characters, following Jolicoeur (1963).

Character	Population			
	All populations	RKB	PISL	HOM
AM	0.3132	0.3157	0.3265	0.1672
AD	0.3037	0.3095	0.3385	0.1447
DG	0.3087	0.3340	0.2589	0.2415
AK	0.3063	0.6240	0.3139	0.2051
GP	0.3302	0.3212	0.4259	0.1548
BJ	0.2635	0.3348	0.3178	0.2051
IW	0.0796	0.2789	0.3457	0.5943
ad	0.3696	0.3301	0.3739	0.4236
ce	0.5469	0.4313	0.2675	0.5015

The mean genetic distance between the Homosassa Bay and Rabbit Key Basin populations was 0.035.

Morphometrics. Standard error estimates for measurements of morphometric characters were universally low, averaging 0.64% of the mean for all variables, suggesting that measurement error did not overly influence the variance in subsequent morphometric analyses.

Scallops from the Pine Island Sound collection were significantly larger than those from Homosassa Bay, and both Pine Island Sound and Homosassa Bay scallops were much larger than those from our Rabbit Key Basin collection (ANOVA, all $p < 0.05$) (figures 2–3). The type specimens of *Argopecten irradians taylorae* were slightly larger than the live specimens from our Rabbit Key Basin collection and similar in size to the empty valves we collected from Rabbit Key Basin, although two pairs of empty valves exceeded 50 mm in height. Representative valves from the sample populations are illustrated in figures 4–7.

Numbers of right-valve plicae were similar for all sample populations that we examined morphometrically, and plical number was not significantly related to valve height ($0.05 < p < 0.06$). However, the effect of population on plical number was significant ($p < 0.0001$), and right-valve plicae were significantly more numerous on Homosassa Bay scallops ($p < 0.05$) than on Rabbit Key Basin and Pine Island Sound scallops. Plical numbers were not significantly different between Rabbit Key and Pine Island Sound populations. Width of plicae relative to valve size was positively related to valve height ($p < 0.0002$).

Patterns of growth for individual mensural characters varied greatly and inconsistently among populations (table 3). Although some characters varied isometrically, there was no consistent trend among populations.

Coloration of valves from all populations was similar; more than 90% of specimens from each population exhibited the color pattern of type E of Elek and Adamkewicz (1990). Variations in color pattern were not significantly different among populations. More than 95% of the valves from each scallop population had white backgrounds, and 100% of the specimens had mottled left valves (table 4). Excluding one yellow and two orange scallops from Rabbit Key Basin and one orange scallop from Pine Island Sound, right valves in all populations were consistently all white except in the early juvenile region of the shell.

The first principal component (PC1) from the standard PCA of all data accounted for 83.3% of the total variance, and the second and third principal components accounted for 7.7% and 4.1%, respectively, of the variance. Burnaby size-corrected PCA showed that principal components 1 through 3 accounted for 59.2%, 14.9%, and 9.8% of total variance, respectively. Two variables in the Burnaby PCA accounted for most of the variance in PC2 and PC3: width of plical interspaces (IW) represented 28.5% of PC2 variance and 69.5% of PC3 variance, and ce (length of ligament insertion) accounted for 33.6% of PC2 variance and 20.4% of PC3 variance (table 5). Plots of PC2 and PC3 from the size-corrected PCA of the data from all 3 populations and including the separate collection of empty valves from Rabbit Key Basin (figure 8) demonstrate that scatterplots from each population overlap with those from all other populations. Particularly extensive overlap occurs between the Rabbit Key Basin and Homosassa Bay populations, and less overlap is seen in plots representing the Pine Island Sound population and those of all other populations.

DISCUSSION

The genetic distance (D = 0.035) between the Homosassa Bay and Rabbit Key Basin populations of *Argopecten*

Table 4. Summary of color and color pattern on valves of *Argopecten irradians* from Rabbit Key Basin (RKB, n = 66), Pine Island Sound (PISL, n = 56), and Homosassa Bay (HOM, n = 60), Florida. Numbers expressed as percentages.

Population	Background color			Rays present		Mottling		Banding	
	White	Yellow	Orange	Left	Right	Left	Right	Left	Right
RKB	95.5	1.5	3.0	90.9	30.3	100	80.3	100	57.6
PISL	98.2	0	1.8	96.4	12.5	100	85.7	41.1	58.9
HOM	100	0	0	98.3	6.7	100	93.3	98.3	90.0
MEAN	97.8	0.5	1.6	95.1	17.0	100	86.3	81.3	68.7

Table 5. Percentage of variance in principal components 2 and 3 from Burnaby PCA attributable to individual valve characters for *Argopecten irradians* populations from Rabbit Key Basin, Pine Island Sound, and Homosassa Bay. Character abbreviations are defined in the appendix.

Character	Principal component 2	Principal component 3
AM	4.78	1.13
AD	3.60	1.73
DG	2.09	0.72
AK	6.86	2.28
GP	9.18	3.09
BJ	8.13	0.20
IW	28.50	69.50
ad	3.28	0.89
ce	33.57	20.43

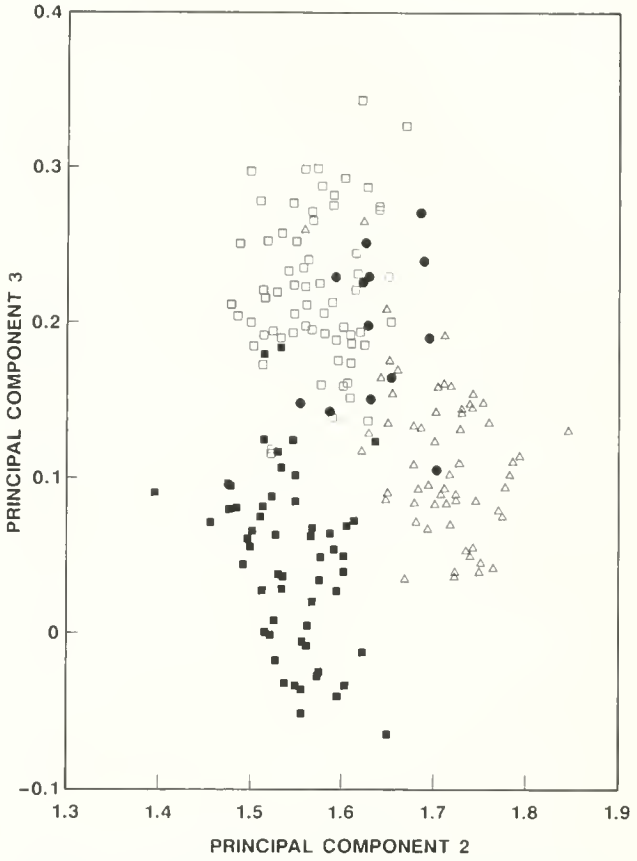


Figure 8. Bivariate scatterplot of principal component 2 and 3 scores generated using Burnaby's (1966) size-corrected principal component analysis on morphometric measurements of *Argopecten irradians* from Rabbit Key Basin (□), Pine Island Sound (■), and Homosassa Bay (△) populations. Population indicated by (●) represents empty valves collected from Rabbit Key Basin locality.

irradians s.l. is on the order of distances between local races (Nei, 1976, 1987). This value is comparable to those between disjunct but apparently recently separated populations of the Baltic clam *Macoma balthica* (Linnaeus, 1758) (Nei's D = 0.058) (Meehan *et al.*, 1989) and between Great Barrier Reef and Enewetak Atoll populations of the giant clam *Tridacna maxima* (Nei's D = 0.033) (Ayala, 1975). Electrophoretic data from five additional populations of *Argopecten irradians s.l.* examined by Krause (1992) (Martha's Vineyard, Massachusetts; Niantic River, Connecticut; Orient Harbor, Long Island, New York; Core Banks, North Carolina; and St. Joseph Bay, Florida), treated identically, were used along with data from the Rabbit Key Basin and Homosassa Bay populations to create a genetic distance matrix. A dendrogram was constructed from the genetic distance matrix using the unweighted pair-group method with arithmetic mean (UPGMA Sneath & Sokal, 1973), provided by the computer program NTSYS (Applied Biostatistics, Inc.) (figure 9). Standard errors of tree branching points were estimated using the procedure of Nei *et al.* (1985) who point out that, when using electrophoretic data and less than 30 loci, the topology of a reconstructed tree is subject to a large stochastic error. The size of the errors allows us little confidence in the dendrogram, but two factors may contribute to an inflation of the estimated standard errors. When genetic distance values are very low, less than 0.105, the value of I in the equation $D = -\log_e I$ exceeds 0.9. When $I > 0.9$ and average heterozygosity (MLH) is >0.2 serious overestimation of the variance may occur (Nei *et al.*, 1985). Twelve of 21 pairwise I values in the scallop genetic distance matrix exceed 0.9 and MLH = 0.44 p. Despite the size of the standard errors, the genetic distance data indicate a close relationship between the Rabbit Key Basin and Homosassa Bay scallops within *Argopecten irradians*.

The small but significant differences in allele frequency between Homosassa Bay and Rabbit Key Basin populations at the AP and LAP loci might be evidence for localized selection among genotypes between these sites (McMillen *et al.*, 1994), for reduced gene flow between the populations (Beaumont & Zouros, 1991), or some combination of these processes. The overall magnitude of genetic variation among the Florida populations is only slightly greater than that found among Krause's (1992) northern populations of *A. i. irradians*. Therefore *A. i. taylorae* appears, based on genetic evidence, not to differ at the subspecific level from other Florida populations examined.

Values for the mean percentage of heterozygous loci per individual (MLH) in the Homosassa Bay (43%) and Rabbit Key Basin (44%) populations are relatively high but similar to the 45.3% MLH reported by Bricelj and Krause (1992) for *Argopecten irradians irradians* from the Niantic River estuary, Connecticut. These values indicate that high MLH values may be characteristic of *Argopecten irradians s.l.*, but Wall *et al.* (1976) reported a MLH of 11.6% for *A. irradians* from Bogue Sound, North Carolina. Values of MLH reported for 5 other pectinids range from 9.4% to 32.1% (Nikiforov & Dolgonov, 1982; Beaumont & Beveridge, 1984).

Color in *Argopecten irradians* is genetically controlled

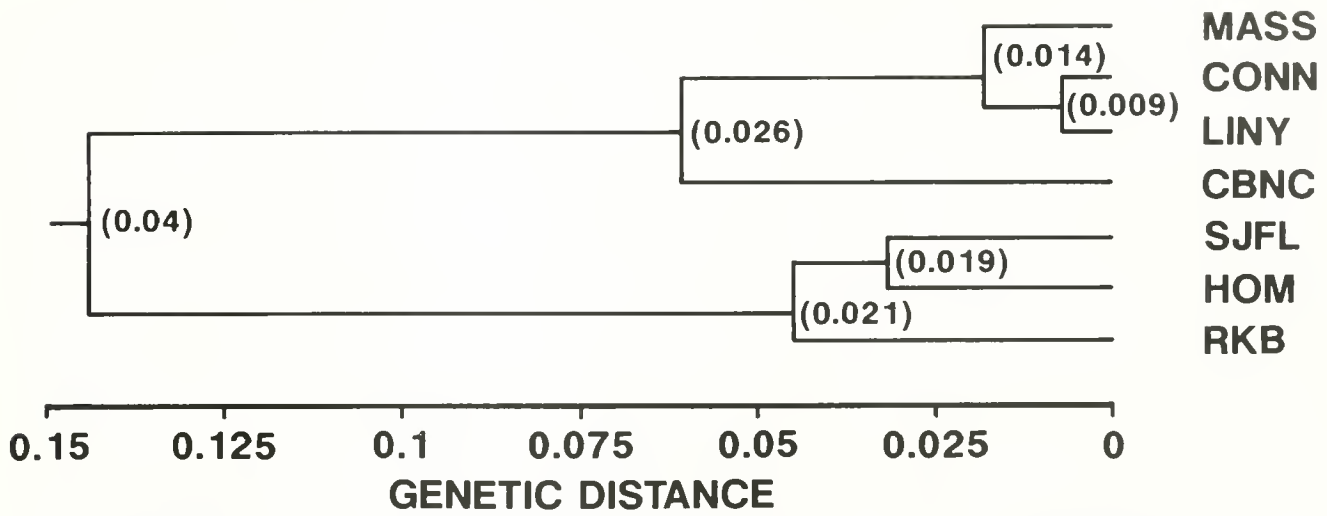


Figure 9. UPGMA tree constructed from the Nei (1972) genetic distance matrix for populations of *Argopecten irradians*. Population abbreviations are MASS: Martha's Vineyard, Massachusetts; CONN: Niantic River, Connecticut; LINY: Orient Harbor, Long Island, New York; CBNC: Core Banks, North Carolina, SJFL: St. Joseph Bay, Florida; HOM: Homosassa Bay, Florida; RKB: Rabbit Key Basin, Florida. Numbers in parentheses are standard errors of branching points estimated using the procedure of Nei *et al.* (1985).

and may sometimes be useful in distinguishing individuals and populations (Kraeuter *et al.*, 1984; Adamkewicz & Castagna, 1988). Nevertheless, we found no substantial differences in valve coloration or color pattern between the Homosassa Bay, Pine Island Sound, and Rabbit Key Basin scallop populations to support Petuch's (1987) contention that shells of *A. i. taylorae* are much more colorful than those of *A. i. concentricus*. Most scallops in each of the populations had a rayed pattern on the left valve, and additional color was generally expressed as mottling and banding, somewhat obscuring the rayed pattern. Variations in the intensity of color were affected by the nature and extent of fouling on the left valve and possibly by ontogenetic change.

Petuch (1987) identified the small size of scallops from the Rabbit Key Basin population as an important character that distinguishes *Argopecten irradians taylorae* from *A. i. concentricus*. Although heights of live scallops from our Rabbit Key Basin collection were significantly smaller than those in all other collections, the empty valves that we collected from the same locality were comparable in size to those in Petuch's type series. This suggests that the scallops in Rabbit Key Basin may indeed be distinctively smaller than other Florida scallops, although the close genetic similarity between the Rabbit Key Basin and Homosassa Bay populations indicates that scallop size is readily influenced by local conditions. The small size of our live Rabbit Key Basin collection coupled with the heterozygote deficits at the loci ODH and PGM that occurred among the scallops from this collection [similar to deficits at these loci that have been reported for juveniles of other species of Pectinidae (Volckaert & Zouros, 1989; Bricelj & Krause, 1992)] may indicate that the scallops we collected from Rabbit Key Basin were juveniles.

Discontinuities in plical number occur between populations of *Argopecten irradians* along the geographic range of the species, and these differences have been emphasized taxonomically (Clarke, 1965). The number of plicae ranges from 12 to 25 in the described subspecies (Clarke, 1965; Waller, 1969; Abbott, 1974; Petuch, 1987) and is reportedly under genetic control (Kraeuter *et al.*, 1984). We substantiate the elevated plical numbers that have been reported for Florida *A. i. concentricus*, but we did not find even greater plical counts in the Rabbit Key Basin population as reported by Petuch (1987). In fact, the mean plical number for our sample of scallops from Rabbit Key Basin was statistically indistinguishable from that of scallops from Pine Island Sound. Higher counts of plicae for the type series reported by Petuch (1987) suggest that he may have misidentified as plicae some of the "riblets" that occur on the disk flanks of this species; such confusion has been previously reported by Clarke (1965) and Waller (1969). Our analysis of right valve plical numbers rejects the conclusion that scallops from Rabbit Key Basin represent a separate and unique subspecies.

Width of the plicae at the ventral margin was identified by Petuch (1987) as a character that can be used to separate *Argopecten irradians taylorae* from *A. i. concentricus*. However, because plical width relative to valve size is positively correlated with valve height, its use in a univariate comparison of scallops of different sizes without accounting for allometry is invalidated. Moreover, our data indicate that Rabbit Key Basin scallops have relatively narrower plicae than do scallops from Homosassa Bay or Pine Island Sound—not wider as reported by Petuch.

Inconsistencies in the relationship between growth and valve characters between populations indicate that morphometric characters do not vary with growth in a simple manner; variability due to small sample sizes and mea-

surement error may also affect the allometric coefficients (Marcus, 1990). Regardless of the source, the inconstancy of shape variables and the presence of allometric relationships among mensural characters, morphometric ratios, and size cast doubt upon the use of univariate characters in describing morphometric differences between scallop populations, adding empirical emphasis to warnings by previous authors (summarized in Humphries *et al.*, 1981).

Burnaby size-corrected PCA failed to distinctly separate the Rabbit Key Basin, Pine Island Sound, and Homosassa Bay scallop populations. Although morphometric overlap among populations is evident in the plots of PC2 and PC3, scatterplots of the individual populations form distinct clusters and indicate that the more geographically distant populations (Rabbit Key Basin and Homosassa Bay) in our samples were morphometrically more similar. Variation in shape, and hence some separation in the plots of PC2 and PC3, may be influenced by ontogeny of individuals, because the Burnaby technique does not completely remove the effect of size (Humphries *et al.*, 1981), but separation on the basis of shape variables indicates that scallop shape is heavily influenced by local conditions and may simply reflect ecophenotypic variation.

We assessed alleged differences between typical *Argopecten irradians taylorae* and representatives of other bay scallops from peninsular Florida. Based on the results of our electrophoretic and morphometric examinations, we refute those differences and conclude that bay scallops from Rabbit Key Basin do not represent a subspecific taxon distinct from Florida populations of *A. i. concentricus*.

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APPENDIX I

Table of morphological characters and abbreviations used in this study, following Waller (1969). Abbreviations refer to either right or left-valve; apostrophes are added in text to indicate left valve measurements.

AM	Valve height
AD	Length of posterior portion of valve
DG	Length of anterior portion of valve
AK	Height of posterodorsal portion of valve
GP	Height of anterodorsal portion of valve
DF	Length of anterior ligament
CD	Length of posterior ligament
EI	Height of anterior auricle
BJ	Height of posterior auricle
DE	Length from valve midline to ventral insertion of anterior auricle
LO	Valve width
ad	Height of resilial insertion
ce	Length of resilial insertion
PW	Width of medial plicae at ventral margin
IW	Width of medial interplical spaces at ventral margin

Subspecific Status of *Argopecten irradians concentricus* (Say, 1822) and of the Bay Scallops of Florida

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ABSTRACT

Nei genetic distances between Florida and North Carolina populations of bay scallops, all putatively *Argopecten irradians concentricus*, are greater than distances between the North Carolina population and populations of *A. i. irradians* from New York to Massachusetts. The subspecies *A. i. concentricus* is probably untenable. Evidence for a subspecies, *A. i. taylorae*, in Florida and the eastern Gulf of Mexico is discussed.

Key words: *Argopecten*, bay scallops, genetics, Pectinidae, subspecies.

INTRODUCTION

Bay scallops, *Argopecten irradians* (Lamarck, 1819), range from New England to Florida, Texas, and northeastern Mexico. Northern, southern, and western populations have been accorded subspecific rank as *A. i. irradians*, *A. i. concentricus* (Say, 1822), and *A. i. amplicostatus* (Dall, 1898) (Clarke, 1965; Waller, 1969). We have found no morphometric or genetic characters to separate scallops of a recently proposed fourth subspecies, *A. i. taylorae* Petuch, 1987, from other Florida populations (Marelli *et al.*, 1996) customarily assigned to *A. i. concentricus*. However, our work shows that Nei (1972) genetic distances between Florida populations and a North Carolina population of *Argopecten irradians*, all putatively of *A. i. concentricus*, are greater than distances between that North Carolina population and populations of *A. i. irradians* from Massachusetts, Connecticut, and New York (figure 1), prompting us to review and reassess the subspecific status of *A. i. concentricus*.

Say (1822) described *Pecten concentricus* based upon specimens from the coast of New Jersey and also recognized as distinct a variety from New England that he named *Pecten borealis*; the latter name is now known to be a junior synonym of *A. i. irradians*. Because Say's specimens of *P. concentricus* are lost, Clarke (1965) selected a neotype from Great Egg Harbor near Atlantic City in southeastern New Jersey, thereby fixing the type locality. Clarke also restricted the type locality of *P. irradians* to Waquoit Bay near Falmouth, Massachusetts.

Clarke (1965) evaluated the status of subspecific units among bay scallops by comparing four "primary characters" [plical count; width/length; height/length; and color (% white)] of shells from 23 populations throughout the range of what he called "the *Argopecten irradians* superspecies." Clarke's results, derived from relatively few specimens ($\bar{x} = 13$) of disparate sizes (height range: 17.7 to 80.6 mm), must be viewed with uncertainty because of our findings of allometric variability among individual populations (Marelli *et al.*, 1996). Nevertheless, Clarke's four samples from the "New Jersey coast"; Atlantic City, New Jersey; Sinepuxent Bay, Maryland; and Hog Island, Virginia are instructive in understanding his concept of *A. i. concentricus*. The New Jersey coast sample (depicted as northern New Jersey but actually unlocalized) had characters consistent with four other samples from Massachusetts and Rhode Island (i.e., *A. i. irradians*); the Atlantic City and Sinepuxent Bay samples shared characters of both the more northern and more southern (North Carolina) samples; and the Hog Island sample grouped with two samples from North Carolina, which in turn most resembled five samples from the eastern Gulf of Mexico between Sanibel Island, Florida, and Ft. Morgan, Alabama. A specimen from Chandeleur Island, Louisiana, was depicted as intermediate between those of eastern and western Gulf (Matagorda, Texas, to Tampico, Mexico; i.e., *A. i. amplicostatus*) populations, but its plical count was clearly assignable to the eastern group.

Clarke interpreted his results to indicate that northern,

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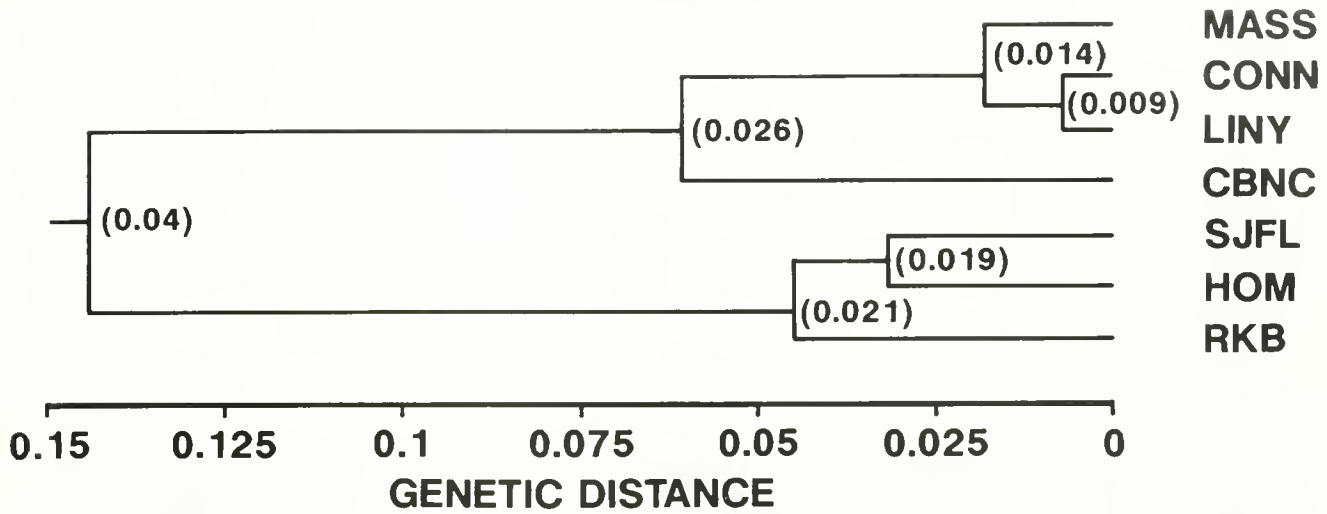

Figure 1. UPGMA tree constructed from the Nei (1972) genetic distance matrix for populations of *Argopecten irradians*. See Marelli *et al.* (1996) for methods. Abbreviations are MASS: Martha's Vineyard, Massachusetts; CONN: Niantic River, Connecticut; LINY: Orient Harbor, Long Island, New York; CBNC: Core Banks, North Carolina; SJFL: St. Joseph Bay, Florida; HOM: Homosassa Bay, Florida; RKB: Rabbit Key Basin, Florida. Numbers in parentheses are standard errors of branching points estimated using procedures of Nei *et al.* (1985).

southern, and western populations of *A. irradians* are morphologically dissimilar throughout most of their ranges but that they intergrade between New Jersey and Virginia and again in Louisiana. Despite the transitional features of scallops in the type population, Clarke tried to maintain nomenclatural stability by retaining the name *concentricus* for the economically important subspecies of the southern United States. In retrospect, Clarke's findings seem to have provided more support for the existence of clines than for the existence of subspecies.

The subspecies concept is regarded by some as arbitrary because it attempts to separate populations that, in fact, may show gradual transitions in morphology, physiology, and genetics over the range of a species (Wilson & Brown, 1953; Endler, 1977). The classification of *Argopecten irradians* exemplifies difficulties inherent in attempts to distinguish such populations. The genetic distances we report for bay scallops from Florida to Massachusetts could indicate a cline among populations between which no clear boundaries exist, and that is probably the case among the Atlantic coast populations north of Florida. The transitional nature of morphological characters of the type population of *A. i. concentricus* seems to support that explanation, as do genetic similarities we found among populations between North Carolina and Massachusetts. Thus, the concept of *A. i. concentricus* as a subspecies seems untenable.

The subspecies concept gains strength, however, when it is applied to populations that are separated by distributional gaps or barriers that constrain contact (*sensu* Mayr, 1969). Waller (1969) described a distributional gap of approximately 764 km (475 miles) between the easternmost population of *A. i. amplicostatus* and the westernmost population he considered to represent *A. i. concentricus*, and he proposed that the Mississippi Delta acts as a barrier to genetic interchange between those stocks. Thus, subspecific designations for those populations seem appropriate.

A distributional gap of similar magnitude in the southeastern United States has received less attention, perhaps because it contains no obvious barrier. The northernmost population of bay scallops along eastern Florida is at Palm Beach Inlet (Lake Worth Inlet) (Waller, 1969) near latitude 26°45′N, and the next documented occurrence of the species seems to be at Lockwood Folly Inlet near Cape Fear, North Carolina (Porter, 1974), near 33°50′N; these populations are separated by a minimum distance of nearly 800 km. Even if reports of uncommon occurrence in South Carolina (Clarke, 1965; Shoemaker *et al.*, 1978) and an unsubstantiated report from Georgia (Petuch, 1987) are considered, no population of bay scallops is known in the region between Palm Beach Inlet and the Florida-Georgia border at 30°45′N, a gap of nearly 450 km. Thus, despite reported similarities in shell morphology, the genetic gap between the North Carolina and Florida stocks is not a simple expression of distant populations separated by other, more contiguous populations distributed along a cline. Instead, the bay scallop stocks of Florida (and probably those extending to eastern Louisiana) seem to comprise an aggregation of populations isolated by large distances from other aggregations to the north and to the west, i.e., a subspecies, *sensu* Mayr (1969).

If *A. i. concentricus* is not appropriate as a name for bay scallop stocks of Florida and the eastern Gulf of Mexico, and if those stocks merit subspecific recognition, then *A. i. taylorae* Petuch, 1987, is the first available name. Another possibility, *Pecten circularis* Sowerby, 1835, was shown by Waller (1995) to be a junior synonym of *Argopecten irradians concentricus*. Dr. Waller in-

formed us (in litt., 1/30/96) that the holotype of *Pecten circularis* "compares favorably with North Carolina *concentricus* in overall shape, auricular shape, rib shape, and rib count, and it differs in these features from Gulf populations."

We advocate caution to those who might immediately apply the name *Argopecten irradians taylorae* for the Florida and eastern Gulf stocks. Our study (Marelli *et al.*, 1996) was intended only to assess differences between typical *A. i. taylorae* and other bay scallops of Florida. Those differences were refuted using analytical techniques involving both genetics and morphometrics. Similar work is needed to elucidate the genetic compositions of populations in the transition zone between New Jersey and Virginia, in South Carolina and Georgia (if such populations exist), in the region between northwestern Florida and eastern Louisiana, and in the western Gulf of Mexico (*A. i. amplicostatus*) to provide perspective for evaluating genetic distances among all of the populations before the question of subspecies is resolved.

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Distribution of Unionoid (Bivalvia) Faunas in Minnesota, USA

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ABSTRACT

The freshwaters of Minnesota are significant because they form the conjunction of three major drainage systems: the Mississippi, the St. Lawrence, and Hudson Bay; 46 species of freshwater mussels (Bivalvia: Unionoidea) inhabit these rivers and lakes. Of these, 31 are found only in the Mississippi River and its tributaries below Minneapolis. Nine species have distributions that include all of the state's drainage systems, 5 species have been reliably reported from only the Red River of the North and Lower Mississippi River drainage systems; and *Elliptio complanata* is found only in the Lake Superior Basin. Problematical records within the state are addressed.

Key words: Biogeography, Unionidae, Margaritiferidae, freshwater mussels.

INTRODUCTION

> No equal area on earth has such a diversity of Naiad life or such magnificent shells. Here are found the largest species in the world; here are forms with knobs, pustules, angles, lobes, and concentric sculpture. The nacre of many of them is wonderfully rich in tints of silver, pink, purple, salmon or red, and it is equaled in beauty by the elegant patterns of external painting, in stripes and mottlings and delicate hair lines.
>
> Charles T. Simpson (1896) on the Unionoidea of the Mississippi Valley

The distributions of the 46 species of freshwater mussels (Bivalvia: Unionoidea) that inhabit Minnesota were presented by Charlotte Webster Dawley in her doctoral thesis (1944) and a widely cited paper (Dawley, 1947). However, additional data have accumulated in the nearly half century since then. This paper seeks to update the literature record and establish the known distributions of these mollusks.

The life-cycle of a freshwater mussel involves the use of one or more species of fish or, in one case, an amphibian as a host for the parasitic larva or glochidium. In general, the major phase of dispersal occurs via parasitism of their host. Thus, barriers that inhibit the vagility of fish (drainage divides, waterfalls, etc.) also block the dispersal of the Unionoidea.

Hydrology of Minnesota. Minnesota's surface area of 218,500 km^2 is drained by three divergent watersheds (Figure 1). The Lake Superior System, the smallest, drains to the St. Lawrence River via Lake Superior. It is defined as the lake itself and all it's Minnesota tributaries. This system drains about 15,300 km^2 or 7% of the state.

The next largest watershed, draining 76,500 km^2 or 35% of the state, runs to Hudson Bay and is subdivided into the Red River System (the Red River of the North and all its Minnesota tributaries) and the Lake of the Woods System (the Rainy River and all Minnesota waters draining to Lake of the Woods). The two systems are confluent at Lake Winnipeg, Manitoba, but because they have different mussel faunas, they are considered separately.

The remaining 126,700 km^2 (58%) drains to the Gulf of Mexico via the Mississippi River. The basin is subdivided into the Upper and Lower Mississippi River Systems (following Underhill, 1989) based on their divergent histories and vastly disparate mussel faunas. The Upper Mississippi River System is that portion of the Mississippi River and all of its tributaries above the Falls of St. Anthony at Minneapolis. The Lower Mississippi River System is the river and all of its Minnesota tributaries below the Falls of St. Anthony. This includes not only those watersheds draining directly into the Mississippi River in Minnesota (the St. Croix, Minnesota, Zumbro, Cannon, and Root River Watersheds), but also those waters in southwestern Minnesota draining to the Missouri and Des Moines Rivers.

For the purposes of this study, state boundaries formed by streams extend to the opposite bank to relax possible political tensions among mussels on opposing sides of the same river.

These five drainage systems were in place following the final northward retreat of Glacial Lake Agassiz. Before that time, the enormous volumes of meltwater left

Figure 1. The Drainage Systems of Minnesota. The Red River System (RRS) and Lake of the Woods System (LWS) are confluent at Lake Winnipeg, eventually emptying to Hudson Bay. The Lake Superior System (LSS) drains to the Great Lakes. The remainder of the state drains via the Mississippi and is comprised of the Upper Mississippi River System (UMRS) and Lower Mississippi River, Minnesota River, and St. Croix River subsystems (LMRS, MRS, and SCRS, respectively). See text for explanation of the state's drainage systems.

in the wake of wasting glaciers over-ran present drainage divides and connected now dissociated basins. At such times, unionoids were free to migrate up the Mississippi River from southern refugia (Johnson, 1980) and into adjacent basins until water levels receded.

MATERIALS AND METHODS

Species have been assigned to watersheds using not only specimens housed in the University of Minnesota's James Ford Bell Museum of Natural History (JFB) Invertebrate Collection but also from an extensive literature survey. In the Appendix, for each species, a single lot is listed for each basin when available, generally those used by earlier authors.

The following literature references where utilized to establish the distributions of the Unionoidea in each of the above defined Minnesota drainage systems. No archeological or fossil literature has been included.

Lake Superior System: Dall (1905), Dawley (1944, 1947), Goodrich and van der Schalie (1932: Lake Superior in general), Moyle (1947), Walker (1913).

Lake of the Woods System: Baker (1929, 1935), Clarke (1973), Dawley (1944, 1947).

Red River System: Baker (1929), Clarke (1973), Coker and Southall (1915), Cvancara (1966, 1967, 1970, 1977, 1979, 1983), Cvancara *et al.* (1981), Daniels (1909), Dawley (1944, 1947), Grant (1885), MN DNR (1984, 1986), Radke (1992), Sargent (1895), Wilson and Danglade (1914).

Upper Mississippi River System: Baker (1929), Bright (1988), Dawley (1944, 1947), Grant (1885), Moyle (1940), Sargent (1895), Wilson and Danglade (1914).

Lower Mississippi River Subsystem: Baker (1928), Bright (1988), Bright *et al.* (1989), Coon *et al.* (1977), Cooper (1834), Davis (1990), Dawley (1944, 1947), Fuller (1978, 1980), Grant (1885), Grier (1922, 1926), Grier and Mueller (1922); Havlik (1981), Holzinger (1887), Hornbach *et al.* (1992), Johnson (1980), Mathiak (1979), Nachtrieb (unpublished), Southall (1925), Thiel (1981), van der Schalie and van der Schalie (1950), Wilson and Danglade (1914).

Minnesota River Subsystem: Bright *et al.* (1990), Dawley (1944, 1947), Grant (1885), MN DNR (1985), Nachtrieb (unpublished), Wilson and Danglade (1914).

St. Croix River Subsystem: Baker (1928), Bright (1988), Cooper (1834), Dawley (1944, 1947), Fuller (1978, 1980), Imlay (1972), Mathiak (1979), Stern (1983), Wilson and Danglade (1914).

Wilson and Danglade (1912) and Ellis (1931), provided only vernacular names, but these have been reworked in a scientific context by Wilson and Danglade (1914) and van der Schalie and van der Schalie (1950), respectively. Grant (1887) reported collecting unnamed *Anodonta* and *Lampsilis* from unspecified watersheds of the Arrowhead Region of northeastern Minnesota. Few data are available on the Unionoidea of the Lake Superior System. Of the general Great Lakes literature reviewed (e.g., van der Schalie, 1961; Walker, 1913), most study has centered on the eastern lakes, emphasizing Lake Erie. The references cited above provide almost no information on the mussels found in the streams of the North Shore of Lake Superior (with the exception of the St. Louis River). Smith and Moyle (1944), however, surveyed the fauna of these streams, including the macrobenthos, and reported no unionoids. Since Moyle, in his other reports (1940, 1947), has provided mussel data it can be assumed that no unionoids are present in these streams.

For mussel distributions adjacent to Minnesota, the reader is referred to the following references: North Dakota: Cvancara (1966, 1967, 1970, 1975, 1976, 1983), Cvancara *et al.* (1966, 1972, 1976); South Dakota: Coker and Southall (1915), Over (1913); Canada: Clarke (1973, 1981); Wisconsin: Baker (1928), Havlik and Stansbery, (1977), Mathiak (1979), Stern (1983).

RESULTS

Figure 2 presents the distributions of the Unionoidea in Minnesota. For each species, the systematic assignment follows Williams *et al.* (1993), which claims to provide

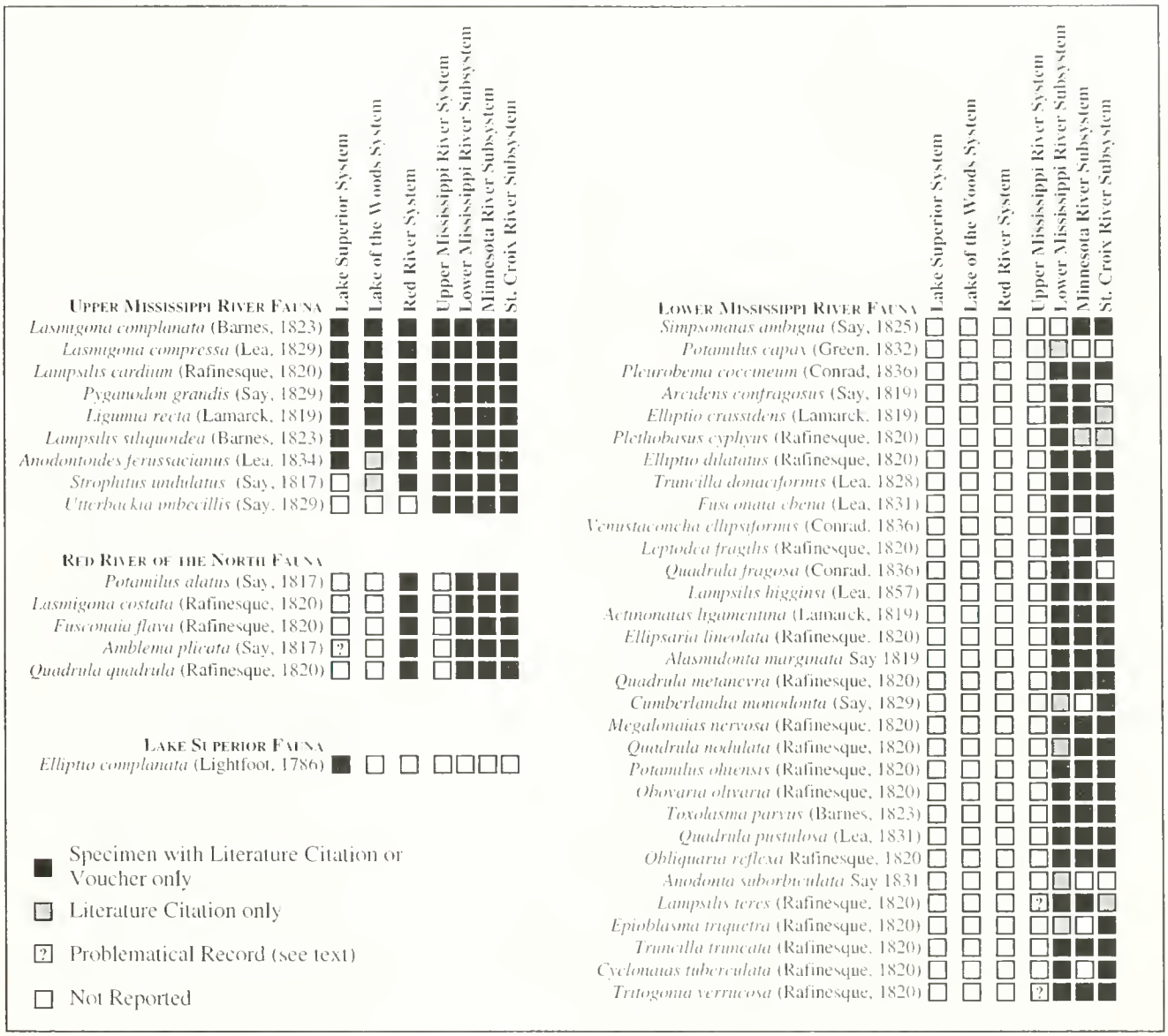
Lake Superior System
Lake of the Woods System
Red River System
Upper Mississippi River System
Lower Mississippi River Subsystem
Minnesota River Subsystem
St. Croix River Subsystem
Upper Mississippi River Fauna
Lasmigona complanata (Barnes, 1823)
Lasmigona compressa (Lea, 1829)
Lampsilis cardium (Rafinesque, 1820)
Pyganodon grandis (Say, 1829)
Ligumia recta (Lamarck, 1819)
Lampsilis siliquoidea (Barnes, 1823)
Anodontoides ferussacianus (Lea, 1834)
Strophitus undulatus (Say, 1817)
Utterbackia imbecillis (Say, 1829)
Red River of the North Fauna
Potamilus alatus (Say, 1817)
Lasmigona costata (Rafinesque, 1820)
Fusconaia flava (Rafinesque, 1820)
Amblema plicata (Say, 1817)
Quadrula quadrula (Rafinesque, 1820)
Lake Superior Fauna
Elliptio complanata (Lightfoot, 1786)
Specimen with Literature Citation or Voucher only
Literature Citation only
Problematical Record (see text)
Not Reported
Lower Mississippi River Fauna
Simpsonaias ambigua (Say, 1825)
Potamilus capax (Green, 1832)
Pleurobema coccineum (Conrad, 1836)
Arcidens confragosus (Say, 1819)
Elliptio crassidens (Lamarck, 1819)
Plethobasus cyphyus (Rafinesque, 1820)
Elliptio dilatatus (Rafinesque, 1820)
Truncilla donaciformis (Lea, 1828)
Fusconaia ebena (Lea, 1831)
Venustaconcha ellipsiformis (Conrad, 1836)
Leptodea fragilis (Rafinesque, 1820)
Quadrula fragosa (Conrad, 1836)
Lampsilis higginsi (Lea, 1857)
Actinonaias ligamentina (Lamarck, 1819)
Ellipsaria lineolata (Rafinesque, 1820)
Alasmidonta marginata Say 1819
Quadrula metanevra (Rafinesque, 1820)
Cumberlandia monodonta (Say, 1829)
Megalonaias nervosa (Rafinesque, 1820)
Quadrula nodulata (Rafinesque, 1820)
Potamilus ohiensis (Rafinesque, 1820)
Obovaria olivaria (Rafinesque, 1820)
Toxolasma parvus (Barnes, 1823)
Quadrula pustulosa (Lea, 1831)
Obliquaria reflexa Rafinesque, 1820
Anodonta suborbiculata Say 1831
Lampsilis teres (Rafinesque, 1820)
Epioblasma triquetra (Rafinesque, 1820)
Truncilla truncata (Rafinesque, 1820)
Cyclonaias tuberculata (Rafinesque, 1820)
Tritogonia verrucosa (Rafinesque, 1820)

Figure 2. The Distribution of Unionoid Faunas in Minnesota.

the same list as Turgeon *et al.* (1988) but with spelling and other such errors corrected. Figures depicting these mollusks can be found in Cummings and Mayer (1992) and Fuller (1985). The only exception, *Elliptio complanata* (Lightfoot, 1786), is illustrated in Clarke (1973: 56–57, plate 3). The species list includes only those species verified to occur in Minnesota; distributions presented exclude erroneous records (see Problematical Records below).

The Lower Mississippi Drainage System is divided into three subsystems: the Lower Mississippi River Subsystem, excluding the Minnesota and St. Croix River watersheds; the Minnesota River Subsystem, which includes the main stem of the river and all its tributaries; and the St. Croix River Subsystem, also including the main stem of that river and its tributaries.

Questionable and Problematical Records. Problematical records, both from literature reports and JFB specimens, may lead to false hypotheses; those identified by the author are summarized and dealt with below.

Questionable Literature Records. Four species reported from the Red River System are supported by only a single literature citation each: *Quadrula pustulosa* by Coker and Southall (1915), *Pleurobema coccineum* by Wilson and Danglade (1914), *Elliptio dilatata* by Daniels (1909), and *Obliquaria reflexa* by Dawley (1944, 1947). However, no corroborating voucher specimens exist at the JFB and none of these species were collected by Cvancara (1966, 1967, 1970, 1975, 1976, 1983; Cvancara *et al.*, 1966; 1972; 1976) or others (e.g. Clarke, 1973) who have extensively surveyed basin. *Quadrula pustulosa*, *P. coc-*

cineum, and *E. dilatata* are likely incorrectly identified *Q. quadrula*, *Fusconaia flava*, and *Ligumia recta*, respectively. In the case of *O. reflexa*, both Cvancara (1970) and Clarke (1973) reported personal communications with Dawley in which she admitted her misidentification. The true distributions of these four species are probably limited to only the Lower Mississippi River System.

Problematical Voucher Specimens. The presence of *Tritogonia verrucosa* in the Upper Mississippi River System is indicated by an unpaired valve (JFB 3190) collected by John Moyle (1940). Moyle believed the valve to be evidence of Lower Mississippi species overcoming the Falls of St. Anthony but not surviving because of poor habitat. Dawley (1944, 1947) considered the presence of *Tritogonia* to be an accident, and her opinion is likely correct. Thus, the distribution of *T. verrucosa* is limited to only the Lower Mississippi River System. An unpaired valve of *Amblema plicata* (JFB 7567) was collected from the Cloquet River in the Lake Superior System. However, since *A. plicata* has otherwise not been reported from that system in Minnesota or even from the Lake Superior Basin in general, this single specimen is probably not a remnant of a population and is assumed to be trash or the remains of some introduced individual or individuals. *Amblema plicata* has been reliably reported from only the Red and Lower Mississippi River Systems, and this presumably reflects the mussel's true distribution within the state.

The problematical distribution of *Actinonaias ligamentina* in the Minnesota has been addressed by Clarke (1973). Dawley's Red River specimen could not be located, but records of *A. ligamentina* reported by her (1944, 1947: JFB 2863), Moyle (1940: JFB 2872), and Radke (1992: JFB 7569) have been re-identified as *Lampsilis siliquoidea*. Cvancara (1970) disregarded Dawley's Red River voucher, reporting that in a personal communication, she agreed that her record was probably an error. Thus, *Actinonaias* is limited to only the Lower Mississippi River System.

The single lot, JFB 2332 *Lampsilis teres*, labeled as coming from Leech Lake in the Upper Mississippi River System is likely the result of a cataloging error. Since Dawley (1944, 1947) apparently ignored it, the validity of this record is questionable.

Other Problematical Data. *Utterbackia imbecillis* has never been reported from any of the Lake Superior or Hudson Bay drainage systems. This makes *U. imbecillis* unique among species reliably reported from the Upper Mississippi River System. Also making *U. imbecillis* distinctive is the fact that it may complete its reproductive cycle with or without a glochidial host (Dawley, 1944; Fuller, 1985). This would hamper its upstream vagility, and perhaps *U. imbecillis* could not extend beyond the Upper and Lower Mississippi River Systems before drainage connections were severed.

The presence of *Anodontoides ferussacianus* in the Lake of the Woods System is not supported by a specimen in the JFB, though both Baker (1935) and Dawley (1944, 1947) reported the species from that basin.

Strophitus undulatus has never been reported from the Lake Superior System and its presence in the Lake of the Woods System is supported by only a single literature record: Clarke (1973). Dawley (1944, citing Lefevre & Curtis, 1911) noted that *S. undulatus* is another mussel that can complete its life-cycle independent of a glochidial host. However, the mussel is not obligately anomalous in its reproduction; its widespread distribution indicates that it probably is dispersed by fish at least some of the time. Three of its published glochidial hosts (Hoggarth, 1992) are found in the that watershed as well as Minnesota's four other drainage systems (Underhill, 1989), providing a means of statewide distribution. The apparent absence of *S. undulatus* may actually be the result of the lack of an adequate survey of the St. Louis River System.

DISCUSSION

There is a pattern to the distributions of the Unionoidea in Minnesota. Species with similar distributions can be grouped into faunas; members of each fauna are hypothesized to have shared modes and tempos of dispersal into the state's drainage systems. Ninety-eight percent of the species (45 of 46) are found in the Lower Mississippi River System, supporting the hypothesis that the freshwater mussel fauna of Minnesota dispersed northward from southern refugia by way of the Mississippi River at the close of the Pleistocene (Johnson, 1980). The remaining species, *Elliptio complanata*, appears to have migrated into the state via Lake Superior from the St. Lawrence watershed.

Of the 45 species of unionoids reported from the Lower Mississippi River System, 30 have been reliably recorded from only that system; these mussels constitute the Lower Mississippi River Fauna (Figure 2). Much of this fauna is made up of mussels ecologically limited to larger rivers that were unable to extend their ranges beyond the Lower Mississippi and the lowest reaches of the Minnesota and St. Croix Rivers (e.g., *Fusconaia ebena*, *Ellipsaria lineolata*). Others of the species characteristic of the Lower Mississippi River System may be relatively recent arrivals to the state (e.g., *Anodonta suborbiculata*, *Quadrula nodulata*) since they were not reported by earlier authors.

Those freshwater mussels commonly found above the Falls of St. Anthony are collectively known as the Upper Mississippi River Fauna (Figure 2). The Upper Mississippi River Fauna must have been present at a time when all of the states watersheds were connected. Of the 9 species that belong to this assemblage, only *Utterbackia imbecillis* and *Strophitus undulatus* have not been reported from all five of Minnesota's drainage systems (discussed above).

Five mussel species are found only in the Red and Lower Mississippi River Systems; these belong to the Red River of the North Fauna (Figure 2). At the close of the

Pleistocene, with the formation of Glacial Lake Agassiz, these two drainage systems were connected more than once, and this allowed the dispersal of the Red River of the North Fauna from the Minnesota River basin into that of the Red River of the North.

Elliptio complanata is the only unionoid of the Lake Superior Fauna. It is known only from the Lake Superior System. It has probably migrated into Minnesota in the last 80 years or so from the eastern Great Lakes.

The problematical species discussed above are difficult for exactly the reason that they don not fit neatly into any of the four described unionoid faunas. However, except for the case of *Actinonaias ligamentina*, these problems are the result of single specimens.

Further study of the unionoid faunas of the Lake of the Woods, Lake Superior, and Upper Mississippi River systems promises to advance our knowledge on the distributions of freshwater mussels of the Minnesota region.

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APPENDIX

Figure Citations and Specimens Examined

Provided below are figure references and the James Ford Bell Museum of Natural History (JFB) specimens used to construct Figure 2. For each lot, its catalog number and collection locality are provided. Whenever possible, specimens cited by previous authors have been selected, and these references are cited below. Also provided are corrections and re-identifications with regard to JFB specimens of historical significance.

The following drainage system abbreviations are used:
LMRS = Lower Mississippi River Subsystem
LSS = Lake Superior System
LWS = Lake of the Woods System
MRS = Minnesota River Subsystem
RRS = Red River System
SCRS = St. Croix River Subsystem
UMRS = Upper Mississippi River System

Actinonaias ligamentina (Lamarck, 1819). Figures: Cummings & Mayer (1992:105), Fuller (1985:36). LWS: Dawley's (1944, 1947) Sturgeon River record is JFB 2863 *Lampsilis siliquoidea*. RRS: Radke's (1992) Otter Tail River record is JFB 7569 *Lampsilis siliquoidea*. UMRS: Dawley (1944, 1947) and Moyle's (1940) Crow Wing River record is JFB 2872 *Lampsilis siliquoidea*. LMRS: JFB 2847 Mississippi River, Dresbach, Winona Co.: Dawley (1944, 1947), Grant (1885). MRS: JFB 2859 Minnesota River, New Ulm, Brown Co.: Dawley (1944, 1947). SCRS: JFB 2878 Kettle River, Rutledge, Pine Co.: Dawley (1944, 1947).

Alasmidonta marginata Say, 1819. Figures: Cummings & Mayer (1992:85), Fuller (1985:42). LMRS: JFB 2766 Mississippi River, Winona, Winona Co.: Dawley (1944, 1947), Holzinger (1887). MRS: JFB 2763 Minnesota River: Dawley (1944, 1947). SCRS: JFB 2769 St. Croix River at the mouth of Sunrise River, Chisago Co.: Dawley (1944, 1947).

Amblema plicata (Say, 1817). Figures: Cummings & Mayer (1992:41), Fuller (1985:50). LSS: JFB 7567 Cloquet River, Brimson, St. Louis Co. RRS: JFB 3105 Red River, 20 mi. N of Breckenridge, Wilkin Co.: Dawley (1944, 1947), Grant (1885). LMRS: JFB 3083 Mississippi River, Dresbach, Winona Co.: Dawley (1944, 1947), Grant (1885). MRS: JFB 3093 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885). SCRS: JFB 3112 St. Croix River at the mouth of Sunrise River, Chisago Co.: Dawley (1944, 1947).

Anodonta suborbiculata Say, 1831. Figures: Cummings & Mayer (1992:77), Fuller (1985:58).

Anodontoides ferussacianus (Lea, 1834). Figures: Cummings & Mayer (1992:81), Fuller (1985:57). LSS: JFB 2709 Cloquet River, St. Louis Co. RRS: JFB 6582 Cormorant Lake, Becker Co.: Radke (1992). UMRS: JFB 3995 Rum River, Anoka, Anoka Co.: Dawley (1944, 1947), Grant (1885). LMRS: JFB 2717 Cedar River, Austin, Mower Co.: Dawley (1944, 1947). MRS: JFB 2742 Cottonwood River, Garvin, Lyon Co.: Dawley (1944). SCRS: JFB 2753 Rush Creek: Dawley (1944, 1947).

Arcidens confragosus (Say, 1819). Figures: Cummings & Mayer (1992:89), Fuller (1985:51). LMRS: JFB 2771 Mississippi River, Red Wing, Goodhue Co.: Dawley (1944, 1947). MRS: JFB 2773 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885).

Cumberlandia monodonta (Say, 1829). Figures: Cummings & Mayer (1992:23), Fuller (1985:16). SCRS: JFB 6690 Rush Creek, Rush City, Chisago Co.

Cyclonaias tuberculata (Rafinesque, 1820). Figures: Cummings & Mayer (1992:49), Fuller (1985:10). LMRS: JFB 3198 Mississippi River, Ft. Snelling: Dawley (1944, 1947), Grant (1885). SCRS: JFB 3199 St. Croix River at the mouth of Sunrise River, Chisago Co.: Dawley (1944, 1947).

Ellipsaria lineolata (Rafinesque, 1820). Figures: Cummings & Mayer (1992:107), Fuller (1985:45). LMRS: JFB 2916 Mississippi River, Nininger, Dakota Co.: Dawley (1944, 1947). MRS: JFB 2915 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885). SCRS: JFB 4200 St. Croix River, Taylors Falls, Chisago Co.

Elliptio complanata (Lightfoot, 1786). Figures: Clarke (1973:56–57, plate 3). LSS: JFB 3258 Lake Superior, Duluth, St. Louis Co.: Dawley (1944, 1947).

Elliptio crassidens (Lamarck, 1819). Figures: Cummings & Mayer (1992:67), Fuller (1985:14). LMRS: JFB 3249 Lake Pepin, Goodhue Co.: Dawley (1944, 1947). MRS: JFB 3245 Minnesota River: Dawley (1944, 1947).

Elliptio dilatata (Rafinesque, 1820): the spike. Figures: Cummings & Mayer (1992:69), Fuller (1985:15). LMRS: JFB 3225 Mississippi River, Winona, Winona Co.: Dawley (1944, 1947), Holzinger (1887). MRS: JFB 3242 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885). SCRS: JFB 3244 St. Croix River, Pine Co.: Dawley (1944, 1947).

Epioblasma triquetra (Rafinesque, 1820). Figures: Cummings & Mayer (1992:163), Fuller (1985:44). SCRS: JFB 5701 St. Croix River, Sand Is., Chisago Co.

Fusconaia ebena (Lea, 1831). Figures: Cummings & Mayer (1992:43), Fuller (1985:12). LMRS: JFB 3057 Mississippi River, Dresbach, Winona Co.: Dawley (1944, 1947), Grant (1885). MRS: JFB 6437 Minnesota River, Scott Co.: Bright *et al.* (1990). SCRS: JFB 4044 Lake St. Croix, Washington Co.

Fusconaia flava (Rafinesque, 1820). Figures: Cummings & Mayer (1992:47), Fuller (1985:11). RRS: JFB 3014 Red River, 20 mi. N of Breckenridge, Wilkin Co.: Dawley (1944, 1947), Grant (1885). LMRS: JFB 3045 Mississippi River, Winona, Winona Co.: Dawley (1944, 1947). MRS: JFB 3044 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885). SCRS: JFB 3047 St. Croix River, Marine on St. Croix, Washington Co.: Dawley (1944, 1947).

Lampsilis cardium (Rafinesque, 1820). Figures: Cummings & Mayer (1992:157), Fuller (1985:28). LSS: JFB 2448 Lake Superior, Minnesota Point, Duluth, St. Louis Co.: Dawley (1944, 1947). LWS: JFB 2411 Sturgeon River, Little Fork River watershed, St. Louis Co.: Dawley (1944, 1947). RRS: JFB 2396 Red River, 20 mi. N of Breckenridge, Wilkin Co.: Dawley (1944, 1947), Grant (1885). UMRS: JFB 2400 Mississippi River, Brainerd, Crow Wing Co.: Dawley (1944, 1947), Grant (1885). LMRS: JFB 2397 Mississippi River, Dresbach, Winona Co.: Dawley (1944, 1947), Grant (1885). MRS: JFB 2404 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885). SCRS: JFB 2415 St. Croix River, Marine on St. Croix, Washington Co.: Dawley (1944, 1947).

Lampsilis higginsi (Lea, 1857). Figures: Cummings & Mayer (1992:153), Fuller (1985:33–34). LMRS: JFB 2454 Mississippi River, Dresbach, Winona Co.: Dawley (1944, 1947). MRS: JFB 6396 Minnesota River, Carver Co.: Bright *et al.*, 1990 (cf. *L. higginsi*); Dawley's (1944, 1947) record is JFB 2455 *Obovaria olivaria*. SCRS: JFB 2453 Lake St. Croix, Washington Co.: Dawley (1944, 1947).

Lampsilis siliquoidea (Barnes, 1823). Figures: Cummings & Mayer (1992:151), Fuller (1985:29). LSS: JFB 2291 Cloquet River, St. Louis Co.: Dawley (1944, 1947). LWS: JFB 2983 Sturgeon River, Little Fork River watershed, St. Louis Co.: Dawley (1944, 1947). RRS: JFB 2305 Red River, 20 mi. N of Breckenridge, Wilkin Co.: Dawley (1944, 1947), Grant (1885). UMRS: JFB 2242 Mississippi River, Brainerd, Crow Wing Co.: Dawley (1944, 1947), Grant (1885). LMRS: JFB 2307 Rollingstone Creek, Minnesota City, Winona Co.: Dawley (1944, 1947), Grant (1885). MRS: JFB 2253 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885). SCRS: JFB 2261 St. Croix River at the mouth of Sunrise River, Chisago Co.: Dawley (1944, 1947).

Lampsilis teres (Rafinesque, 1820). Figures: Cummings & Mayer (1992:149), Fuller (1985:31). UMRS: JFB 2232 Leech Lake, Cass Co. LMRS: JFB 2239 Mississippi River, Red Wing, Goodhue Co.: Dawley (1944, 1947). MRS: JFB 2236 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885).

Lasmigona complanata (Barnes, 1823). Figures: Cummings & Mayer (1992:93), Fuller (1985:39). LSS: JFB 3308 Lake Superior, Minnesota Point, St. Louis Co.: Dawley (1944, 1947); Baker (1928): reporting Lea's type-locality. LWS: JFB 3305 Sturgeon River, Little Fork River watershed, St. Louis Co.: Dawley (1944, 1947). RRS: JFB 3302 Red Lake River, Crookston, Polk Co.: Dawley (1944, 1947). UMRS: JFB 7507 Mississippi River, Little Falls public access, Morrison Co. (collected by Bright *et al.*); reported by Dawley (1944) & Grier & Mueller (1922) that Wilson & Danglade (1914) found it in the UMRS; however, the data can not be located in that publication. LMRS: JFB 3301 Mississippi River, Minneiska, Wabasha: Dawley (1944, 1947). MRS: JFB 3299 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885). SCRS: JFB 3289 Lake St. Croix: Dawley (1944, 1947).

Lasmigona compressa (Lea, 1829). Figures: Cummings & Mayer (1992:97), Fuller (1985:41). LSS: JFB 3262 Cloquet River, St. Louis Co.: Dawley (1944, 1947). LWS: JFB 3261 Fall Lake, Lake Co.: Dawley (1944). RRS: JFB 7196 Otter Tail River, Otter Tail Co. (collected by Bright *et al.*). UMRS: JFB 3265 Sauk River, Stearns Co.: Dawley (1944, 1947), Moyle (1940). LMRS: JFB 5251 North Branch Middle Fork Zumbro River, Highway 57 Bridge, Dodge Co.: Bright *et al.* (1989). MRS: JFB 6017 Min-

nesota River, Yellow Medicine Co.: Bright *et al.* (1990). SCRS: JFB 3266 St. Croix River at the mouth of Sunrise River, Chisago Co.: Dawley (1944, 1947).

Lasmigona costata (Rafinesque, 1820). Figures: Cummings & Mayer (1992:95), Fuller (1985:40). RRS: JFB 3279 Red Lake River, Crookston, Polk Co.: Dawley (1944, 1947). LMRS: JFB 3280 Mississippi River, Winona, Winona Co.: Dawley (1944, 1947). MRS: JFB 3274 Minnesota River: Dawley (1944, 1947). SCRS: JFB 4003 Snake River at the mouth of the Groundhouse River, Kanabec Co.

Leptodea fragilis (Rafinesque, 1820). Figures: Cummings & Mayer (1992:121), Fuller (1985:20). LMRS: JFB 2919 Lake Pepin: Dawley (1944, 1947). MRS: JFB 2923 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885). SCRS: JFB 4613 St. Croix River, Marine on St. Croix, Washington Co.

Ligumia recta (Lamarck, 1819). Figures: Cummings & Mayer (1992:137), Fuller (1985:18). LSS: JFB 2205 Lake Superior: Dawley (1944, 1947). LWS: JFB 2214 Lake of the Woods, Pine Is., Lake of the Woods Co.: Dawley (1944). RRS: JFB 2201 Red River, 20 mi. N of Breckenridge, Wilkin Co.: Dawley (1944, 1947), Grant (1885). UMRS: JFB 2994 Mississippi River, Brainerd, Crow Wing Co.: Dawley (1944, 1947), Grant (1885). LMRS: JFB 2989 Mississippi River, Winona, Winona Co.: Dawley (1944, 1947), Holzinger (1887). MRS: JFB 2998 Blue Earth River: Dawley (1944, 1947). SCRS: JFB 2213 Kettle River, Rutledge, Pine Co.: Dawley (1944, 1947).

Megalonaias nervosa (Rafinesque, 1820). Figures: Cummings & Mayer (1992:25), Fuller (1985:52). LMRS: JFB 3071 Mississippi River, Red Wing, Goodhue Co.: Dawley (1944, 1947). MRS: JFB 3065 Minnesota River, Cedar Ave., Hennepin Co.: Dawley (1944, 1947). SCRS: JFB 3063 St. Croix River, Hudson, St. Croix Co., Wisconsin: Dawley (1944, 1947). Lower Mississippi River below Minnesota: Baker (1903).

Obliquaria reflexa Rafinesque, 1820. Figures: Cummings & Mayer (1992:101), Fuller (1985:48). LMRS: JFB 2808 Lake Pepin, Lake City, Wabasha Co.: Dawley (1944, 1947), Grant (1885). MRS: JFB 2489 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885). SCRS: JFB 2804 Lake St. Croix, Washington Co.: Dawley (1944, 1947).

Obovaria olivaria (Rafinesque, 1820). Figures: Cummings & Mayer (1992:109), Fuller (1985:35). LMRS: JFB 2829 Mississippi River, Dresbach, Winona Co.: Dawley (1944, 1947), Grant (1885). MRS: JFB 6520 Minnesota River, Pike Is., Hennepin Co.: Bright *et al.*, 1990; Dawley's (1944, 1947) record is JFB 2832 *Fusconaia ebena*. SCRS: JFB 2826 St. Croix River at the mouth of Sunrise River, Chisago Co.: Dawley (1944, 1947).

Plethobasus cyphyus (Rafinesque, 1820). Figures: Cummings & Mayer (1992:51), Fuller (1985:49). LMRS: JFB 3203 Mississippi River, Dresbach, Winona Co.: Dawley (1944, 1947), Grant (1885).

Pleurobema coccineum (Conrad, 1836). Figures: Cummings & Mayer (1992:59), Fuller (1985:13). LMRS: JFB 3212 Lake Pepin, Goodhue Co.: Dawley (1944, 1947). MRS: JFB 6068 Minnesota River, Chippewa Co.: Bright *et al.* (1990). SCRS: JFB 3219 Snake River: Dawley (1944, 1947).

Potamilus alatus (Say, 1817). Figures: Cummings & Mayer (1992:125), Fuller (1985:25). RRS: JFB 2946 Red River, 20 mi. N of Breckenridge, Wilkin Co.: Dawley (1944, 1947), Grant (1885). LMRS: JFB 2945 Mississippi River, Dresbach, Winona Co.: Dawley (1944, 1947), Grant (1885). MRS: JFB 2941 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885). SCRS: JFB 2957 Snake River, Kanabec Co.: Dawley (1944, 1947).

Potamilus capax (Green, 1832). Figures: Cummings & Mayer (1992:129), Fuller (1985:27). LMRS: Johnson (1980) reporting Green's type locality at St. Anthony Falls, Minneapolis. Lower Mississippi River below Minnesota: Grier & Mueller (1922:9): "...the consensus of opinion is that it ordinarily does not go much north of Davenport, Iowa."

Potamilus ohiensis (Rafinesque, 1820). Figures: Cummings & Mayer (1992:123), Fuller (1985:22–23). LMRS: JFB 2963 Mississippi River, Red Wing, Goodhue Co.: Dawley (1944, 1947). MRS: JFB 2964 Minnesota River, Ft. Snelling: Dawley (1944, 1947); Grant's (1885) record is JFB 2920 *Leptodea fragilis*. SCRS: JFB 5543 St. Croix River, Interstate Park, Chisago Co., Minnesota; Dawley's (1944, 1947) record is JFB 2962 *Leptodea fragilis*.

Pyganodon grandis (Say, 1829). Figures: Cummings & Mayer (1992:79), Fuller (1985:60). LSS: JFB 2471 Comstock Lake, St. Louis Co.: Dawley (1944, 1947). LWS: JFB 2625 Sturgeon Lake, St. Louis Co.: Dawley (1944, 1947). RRS: JFB 2568 Red Lake River, Crookston, Polk Co.: Dawley (1944, 1947). UMRS: JFB 2560 Rum River, Milaca, Mille Lacs Co.: Dawley (1944, 1947), Moyle (1940). LMRS: JFB 3327 Zumbro River, Wabasha, Wabasha Co.: Dawley (1944, 1947), Grant (1885). MRS: JFB 2664 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885). SCRS: JFB 2660 Oxbow Lake, Marine on St. Croix, Washington Co.: Dawley (1944, 1947).

Quadrula fragosa (Conrad, 1836). Figures: Cummings & Mayer (1992:29). LMRS: JFB 3127 Mississippi River, Nininger, Dakota Co. [collected November, 1886 by Winchell; reported as *Q. quadrula* by Dawley (1944, 1947)]. MRS: JFB 6356 Minnesota River, Sibley Co.: Bright *et al.* (1990).

Quadrula metanevra (Rafinesque, 1820). Figures: Cummings & Mayer (1992:35), Fuller (1985:6). LMRS: JFB 3152 Mississippi River, Dresbach, Winona Co.: Dawley (1944, 1947), Grant (1885). MRS: JFB 6357 Minnesota River, Sibley Co.: Bright *et al.* (1990). SCRS: JFB 4607 St. Croix River, Marine on St. Croix, Washington Co.

Quadrula nodulata (Rafinesque, 1820). Figures: Cummings & Mayer (1992:37), Fuller (1985:8). MRS: JFB 6424 Minnesota River, Scott Co.: Bright *et al.* (1990).

SCRS: JFB 4578 St. Croix River, Coppermine Dam, Douglas Co., Wisconsin.

Quadrula pustulosa (Lea, 1831). Figures: Cummings & Mayer (1992:39), Fuller (1985:9). LMRS: JFB 3136 Mississippi River, Winona, Winona Co.: Dawley (1944, 1947), Holzinger (1887). MRS: JFB 3144 Minnesota River, Ft. Snelling: Dawley (1944, 1947). SCRS: JFB 3147 St. Croix River, Marine on St. Croix, Washington Co.: Dawley (1944, 1947).

Quadrula quadrula (Rafinesque, 1820). Figures: Cummings & Mayer (1992:31), Fuller (1985:7). RRS: JFB 3125 Red River, 20 mi. N of Breckenridge, Wilkin Co.: Dawley (1944, 1947), Grant (1885). LMRS: JFB 3121 Mississippi River, Red Wing, Goodhue Co.: Dawley (1944, 1947). MRS: JFB 3122 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885). SCRS: JFB 4911 St. Croix River, Stillwater, Washington Co.

Simpsonaias ambigua (Say, 1825). Figures: Cummings & Mayer (1992:91), Fuller (1985:56). MRS: JFB 6074 Minnesota River, Chippewa Co.: Bright *et al.*, 1990. SCRS: JFB 5063 St. Croix River, Marine on St. Croix, Washington Co.

Strophitus undulatus (Say, 1817). Figures: Cummings & Mayer (1992:83), Fuller (1985:61). RRS: JFB 2784 Red River, 20 mi. N of Breckenridge, Wilkin Co.: Dawley (1944, 1947), Grant (1885). UMRS: JFB 7415 Mississippi River, Crow Wing State Park, Crow Wing Co. (collected by Bright *et al.*). LMRS: JFB 2793 Mississippi River, Red Wing, Goodhue Co.: Dawley (1944, 1947). MRS: JFB 6075 Minnesota River, Chippewa Co.: Bright *et al.* (1990). SCRS: JFB 2795 Grindstone River, Kettle River watershed, Pine Co.: Dawley (1944, 1947).

Toxolasma parvus (Barnes, 1823). Figures: Cummings & Mayer (1992:131), Fuller (1985:54–55). LMRS: JFB 2974 Mississippi River, Wacouta, Goodhue Co.: Dawley (1944, 1947). MRS: JFB 2976 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885). SCRS: JFB 2973 St. Croix River, Marine on St. Croix, Washington Co.: Dawley (1944, 1947).

Tritogonia verrucosa (Rafinesque, 1820). Figures: Cummings & Mayer (1992:27), Fuller (1985:53). UMRS: JFB 3190 Sauk River, St. Cloud, Stearns Co.: Bright (1988), Dawley (1944), Moyle (1940). LMRS: JFB 3189 Mississippi River, Dresbach, Winona Co.: Dawley (1944, 1947), Grant (1885). MRS: JFB 3181 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885). SCRS: JFB 3191 St. Croix River, Taylors Falls, Chisago Co.: Dawley (1944, 1947).

Truncilla donaciformis (Lea, 1828). Figures: Cummings & Mayer (1992:117), Fuller (1985:47). LMRS: JFB 4307 Mississippi River, Northern States Power Prairie Is. Nuclear Generating Plant, 1.5 miles upstream of Lock & Dam #3, Goodhue Co. MRS: JFB 2933 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885). SCRS: JFB 4610 St. Croix River, Marine on St. Croix, Washington Co.

Truncilla truncata (Rafinesque, 1820). Figures: Cummings & Mayer (1992:115), Fuller (1985:46). LMRS: JFB 2896 Mississippi River, Winona, Winona Co.: Dawley (1944, 1947), Holzinger (1887). MRS: JFB 2897 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885). SCRS: JFB 2900 St. Croix River, St. Croix Falls, Polk Co., Wisconsin: Dawley (1944, 1947).

Utterbackia imbecillis (Say, 1829). Figures: Cummings & Mayer (1992:75), Fuller (1985:59). UMRS: JFB 2683 Mississippi River, Fridley, Anoka Co.: Dawley (1944, 1947), Moyle (1940). LMRS: JFB 2682 Lake Pepin, Wacouta, Goodhue Co.: Dawley (1944, 1947). MRS: JFB 2679 Minnesota River, Ft. Snelling: Dawley (1944, 1947), Grant (1885). SCRS: JFB 2768 Oxbow Lake, Marine on St. Croix, Washington Co.: Dawley (1944, 1947).

Venustaconcha ellipsiformis (Conrad, 1836). Figures: Cummings & Mayer (1992:141), Fuller (1985:38). LMRS: JFB 5280 Cascade Creek, Zumbro River watershed, Rochester, Olmsted Co.: Bright *et al.* (1989). SCRS: JFB 5736 St. Croix River, Polk Co., Wisconsin.

The Life and Malacological Contributions of R. Tucker Abbott (1919–1995)

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Dr. Robert Tucker Abbott, one of the best known and most venerated figures in American Malacology, died November 3, 1995 after a protracted battle with pulmonary fibrosis. During his long and multi-faceted career, he was an eminent researcher, curator, editor, museum director, educator, enterpreneur, and an ambassador of his science to a broad and appreciative audience of enthusiastic shell collectors and weekend naturalists.

R. Tucker Abbott was undoubtedly the most widely known malacologist in the world. His unique career has been chronicled like that of no other malacologist. During his life, articles and biographical sketches appeared in *Reader's Digest* [August 1961], *Hawaiian Shell News* 11(5):7 [1963] and again 24(3):3 [1976], *The Wall Street Journal* [March 18, 1994] reprinted in *Hawaiian Shell News* 42(8):7–8 [1994] and *Smithsonian* magazine [August, 1995] as well as in numerous newpaper and shell club articles. Following his death, countless tributes and obituaries have been published, among them those appearing in *American Conchologist*, *Journal of Shellfisheries Research* and *The New York Times*. Most have emphasized the latter portions of his career.

Born on September 28, 1919 in Watertown, Massachusetts, to Charles Matthew (a paint manufacturer) and Frances (a homemaker, nee Tucker) Abbott, Tucker was the third of four brothers. As a boy, Tucker spent his summers in Bermuda, where an uncle, Col. Richard Tucker was Director of the Bermuda Biological Station. It was there that he met and was befriended by Dr. William Beebe, the ichthyologist and pioneer of deep-sea exploration. Dr. Beebe was to have a profound influence on Tucker. Many aspects of Tucker's career as a scientist, popularist, author, and celebrity find parallels in the life of William Beebe.

When Tucker was a young boy, his family moved to Canada. It was there that he and a friend built their first natural history museum in the basement of the Abbott home. Upon graduating from the Humberside Collegiate in Toronto in 1938, Tucker entered Harvard College. While at Harvard, Tucker met Dr. William J. Clench, who was to become his lifelong friend and mentor.

Tucker's career as a malacologist began while he was still an undergraduate at Harvard. He was a Research Assistant in the Department of Mollusks, Museum of Comparative Zoology, Harvard University from 1938–1942. During this time he helped establish the monographic series *Johnsonia*, serving as its first Business Manager, and published his first mongraphs and taxa (co-authored with Clench) prior to graduation. He was given leave from his studies to serve as the malacologist on the Harvard-Archbold Expedition to Melanesia in 1940–41, collecting mollusks in Fiji for three months aboard the junk-yacht *Cheng-Ho*.

After graduating from Harvard College with a B. S. degree in 1942, Tucker became a United States Naval Aviator, and served as a dive-bomber pilot stationed in Guantánamo Naval Station in Cuba until 1944, when he was transferred to the United States Naval Medical Research Unit 2 (NAMRU–2) based in Guam. As the unit's first medical malacologist, Lieutenant Abbott traveled throughout the Marianas, Philippines and the Yangtze Valley of China, examining hundreds of species of freshwater mollusks to identify those capable of acting as intermediate hosts of trematodes parasitic in man, to describe and study the life cycles of these parasites, and to develop effective countermeasures to control them.

In 1946, Tucker left the Navy, married Mary M. Sisler and was appointed Assistant Curator in the Division of Mollusks of the National Museum of Natural History, Smithsonian Institution. In the years that followed, the Abbott family grew with the births of Robert Tucker, Jr., Carolyn Tucker, and Cynthia Douglas. Tucker enrolled in the graduate program of George Washington University, and earned a M. S. degree in 1949, completing his thesis "The Anatomy and Life History of the fresh-water snail, *Thiara granifera* (Gastropoda: Prosobranchiata)" under the direction of Ira B. Hansen. The same year, he was promoted to Associate Curator. Despite maintaining an extensive publication record, Tucker found time in the succeeding years to publish the first edition of *American Seashells* (1954), one of his landmark works, and to complete his Ph. D. at George Wash-

Figure 1. Lieutenant Robert Tucker Abbott, circa 1942.

Figure 2. Mr. R. Tucker Abbott in the mollusk collections of the National Museum of Natural History, Smithsonian Institution, 1950.

ington University. His dissertation, "The Gastropod Genus *Assiminea* in the Philippines" was completed with Paul Simon Galtsoff serving as his faculty advisor.

In late 1954, Tucker left the National Museum of Natural History to fill the newly established Pilsbry Chair of Malacology at the prestigious Academy of Natural Sciences of Philadelphia. Shortly after arriving in Philadelphia, Tucker founded and served as the first president of the Philadelphia Shell Club, as well as Editor of its Proceedings. Following Henry Pilsbry's death in 1957, he became co-editor of *The Nautilus* together with H. B. Baker. In 1959, Tucker established the monographic series *Indo-Pacific Mollusca* as a complement to *Johnsonia*, which dealt with western Atlantic molluscan faunas, and wrote the first three monographs in rapid succession. Under Tucker's leadership, and with support from the Natural Science Foundation, the Department of Malacology enjoyed unprecedented growth, launching collecting expeditions to all areas of the Indo-Pacific ranging from Madagascar to the Cocos-Keeling Islands, the Bay of Bengal, the Philippines and the Cook Islands.

It was in the middle of his stay at the Academy of Natural Sciences that I first met Tucker. He was 40, already at the top of his field, and just returned from the du Pont—Academy of Natural Sciences expedition to the Philippines. My classmate and I were ten years old and very interested in many aspects of natural history. After spending an afternoon with Tucker, we both became avid malacologists and volunteers, a conversion he effected regularly on enthusiasts of all ages.

During the Philadelphia years, Tucker continued to publish prodigiously, yet found time to pursue his hobby, the collection and classification of paper clips. When he appeared as a guest on the television quiz shows "What's My Line?" and "To Tell the Truth" the panel deduced that he was a malacologist, but Tucker was able to elude them when appearing in his capacity as a "clipologist!" Tucker was widowed in 1964 and married Sue Sweeney Darwin in 1966.

Because of his prominence in the field and his large following among collectors, Tucker was recruited by John du Pont to help build a new natural history museum in the suburbs of Wilmington, Delaware. He could not resist the challenge and opportunity to create a new Department of Malacology or a new natural history museum devoted in large part to mollusks. Tucker left the Academy of Natural Sciences of Philadelphia in 1969 to take up the du Pont Chair of Malacology and serve as Assistant Director of the Delaware Museum of Natural History. Calling upon his professional colleagues and friends in the world of amateur conchology, Tucker assembled a collection and library that today is one of the ten largest in the western hemisphere. While at the Delaware Mu-

Figure 3. Dr. R. Tucker Abbott marking proof pages of *Seashells of the World* in his office at the Academy of Natural Sciences of Philadelphia, circa 1962.

Figure 4. A view of Tucker in the specimen preparation room of the Delaware Museum of Natural History, circa 1972. (Photo courtesy of Delaware Museum of Natural History.)

seum of Natural History, Tucker continued as editor of *Indo-Pacific Mollusca*, and assumed primary editorship of *The Nautilus* upon the death of H. B. Baker in 1970. He published numerous papers and books, among them *Kingdom of the Seashell* (1972) and the second edition of *American Seashells* (1974), and was appointed Adjunct Professor at the College of Marine Studies, University of Delaware in 1973. Despite a distance of some 100 miles between the Campus of the College of Marine Studies and the Delaware Museum, Tucker was an active faculty member, teaching graduate courses in Malacology (together with M. R. Carriker) and Evolutionary Biology, and serving on five graduate committees. His students, myself among them, remember his enthusiasm and skill in collecting mollusks in the field, as well as in transforming the "surplus" specimens into a variety of culinary delicacies, including his "Seven Species Soup." Tucker was divorced in 1974. He married Cecelia White in the spring of 1977.

With his monumental accomplishment of museum building behind him, Tucker "retired" to Melbourne, Florida in 1978, to concentrate on writing and to build a successful publishing company, American Malacologists, Inc. Since *Indo-Pacific Mollusca* remained at the Delaware Museum of Natural History, he started another monographic series, *Monographs of Marine Mollusca*, one not encumbered by zoogeographic boundaries. I remember Tucker confiding that, as an undergraduate, he had been torn between pursuing a career in malacology and one in writing. At this point in Tucker's career, his passion for writing clearly blossomed with a seemingly endless profusion of books and articles for the amateur naturalist and collector. His primary mission now more than ever was to reach and educate an ever-expanding audience of avid readers.

By the mid 1980's, Tucker would occasionally talk of retirement, when he would devote his time to gardening and writing about gardening. But that was always "in another five years." Even at this phase of his career, he remained interested and active in various aspects of museum work, consulting with the Florida Museum of Natural History on several exhibits, and completely designing the Hall of Shells at the newly built Fernbank Museum in Atlanta.

When he was in his seventies, which he used to say was middle-aged for a malacologist, Tucker accepted another challenge, to build another museum, this time one devoted entirely to mollusks and emphasizing education and outreach rather than research. Those who were aquainted with Tucker knew that he was never happier than when he had some new project on the drawing boards. He was grateful for having been given the opportunity to call upon the experiences of his long

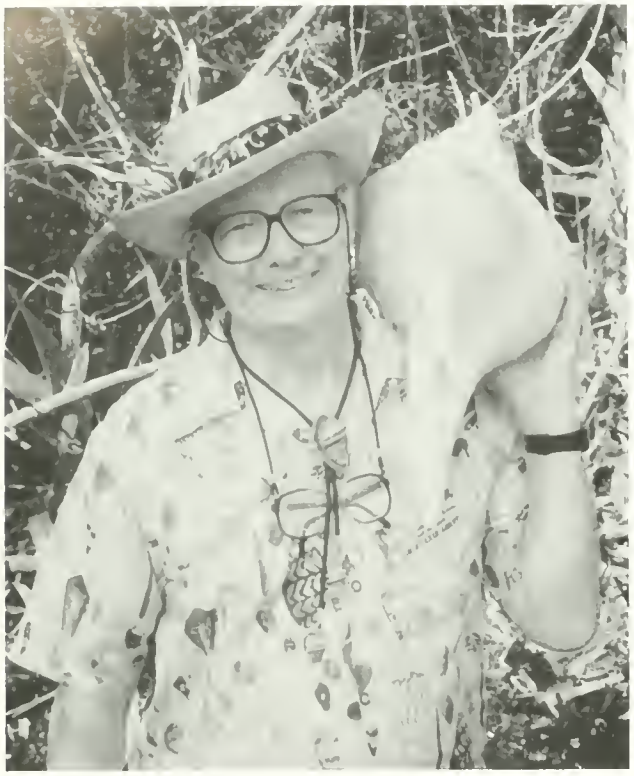

Figure 5. R. Tucker Abbott at the groundbreaking for the Bailey-Matthews Shell Museum, July 6, 1992.

Figure 6. R. Tucker Abbott autographic a copy of one of his books (May, 1992).

and varied career to design a museum that incorporated the best elements of all the museums that he had worked in or visited. First as Consultant to the Board, then as Founding Director, Tucker devoted himself to this new task with extraordinary energy, enthusiasm and intensity. The Bailey-Matthews Shell Museum, which had its formal opening November 18th, barely two weeks after his death, embodies Tucker's concept of the quintessence of what a shell museum should be. He regarded it to be the "crowning accomplishment" of his life.

Many remember Tucker as "Mr. Seashell," a flamboyant man of boundless wit and good humor, described in the *Wall Street Journal* as "partial to short sleeved Hawaiian shirts decorated with brightly colored shells" and wearing multiple pairs of glasses tethered around his neck. He had an enthusiasm that was contagious and the uncanny ability to transform even a casual acquaintance into a co-conspirator in the most far-fetched of projects. Tucker was a man blessed with a love of his work and an unfailing conviction in its importance. For him, the joy was in conceiving and doing a project, rather than its completion. Tucker also had a very strong sense of duty and service to the malacological community. In addition to serving as editor of *The Nautilus* (29 years), *Indo-Pacific Mollusca* (19 years) and *Monographs of Marine Mollusca* (7 years), he was President of the American Malacological Union (1959), Founder and President of The Philadelphia and Wilmington Shell Clubs, Honorary Member of numerous shell clubs in many countries, Secretary of the Society of Systematic Zoology (1956–59), Publications Chairman and later Awards Chairman for the Conchologists of America, Councilman of the Harvard Graduate Society for Advanced Study and Research, Member of the Board of Trustees of the Bermuda Biological Society and the Paleontological Research Institution, and served numerous other organizations in many and varied capacities.

Among his accomplishments, Tucker leaves a legacy of many significant contributions to the infrastructure of malacology in America. He enlarged collections, pioneered curatorial systems, built new museums and Departments of Mollusks, and is responsible for creating at least two positions in the field of malacology. He maintained and created new venues for publication of scholarly works. He trained malacologists by serving on their graduate committees, and by organizing and administering award programs that continue to support students in malacology. Because of his interest in the history of American malacology, he was instrumental in establishing archives now administered by the American Malacological Union and housed at the Academy of Natural Sciences in Philadelphia. Perhaps his most obvious contribution was his strong commitment to popularize the science of malacology and the hobby of shell collecting. He was instrumental in building a large, supportive, well-educated, and well-organized constituency for mollusks, a constituency that few other invertebrate groups enjoy.

In a "Letter to a Beginner," published in American Conchologist [15(2):17], Tucker wrote "You may wonder why I've taken so much time to answer your letter, even though I am 300 years behind in my work and writings. It's because I wrote a letter similar to yours about fifty years ago to a Harvard shell professor, Dr. William J.

Clench. He patiently answered me in detail and started me on the right track. It's my turn to pass on his kindness. I hope you'll have the chance to take your turn." Tucker Abbott has done a great deal for malacology during his life. We would do well to remember his simple request.

R. Tucker Abbott is survived by his wife, Cecilia White Abbott, his son, Robert Tucker Abbott, Jr., his daughters Carolyn Tucker Palmer, Cynthia Douglas Sullivan, Cheryl Robin Nelson, Jonna Leigh Robson, and Erika von der Heyden, and by his brothers John, Matthew and Peter.

ZOOLOGICAL TAXA OF R. TUCKER ABBOTT

Despite a prolific publication record, R. Tucker Abbott proposed relatively few new nomina, these being limited to one family-level taxon, ten genus-level taxa (seven as subgenera) and 71 species-level taxa (19 as subspecies). Of these, 60% of the genus-level taxa and 21% of the species level-taxa were co-authored. Two taxa, the genus *Laevistrombus* and the species *Acanthochitona halesae*, have been attributed to Abbott by subsequent authors because he associated a description and, or figure with a nude name of an earlier author.

Family-Level Taxa

PROPEAMUSSIIDAE Abbott, 1954. American Seashells, p. 369. For *Propeamussium* deGregorio, 1884.

Genus-Level Taxa

Clenchiella Abbott, 1948. The Nautilus 61(3):76. Type species: *Clenchiella victoriae* Abbott, 1948, by original designation. Amnicolidae.

Echininus Clench and Abbott, 1942. Johnsonia 1(4):3. New name for *Nina* Gray, 1850, not *Nina* Horsfield, 1829, nor *Nina* Gray, 1855. Littorinidae.

Fukuia Abbott and Hunter, 1949. Proceedings of the Helminthological Society of Washington 16(2):79–80. Type species: *Fukuia kurodai* Abbott and Hunter, 1949, by original designation. Amnicolidae.

Globivasum Abbott, 1950. As a subgenus of *Vasum* Röding, 1798. Johnsonia 2(28):215–216. Type species: *Turbinella nuttingi* Henderson, 1919, by original designation. Turbinellidae.

Laevistrombus Abbott, 1960. As a subgenus of *Strombus* Linné, 1758. Indo-Pacific Mollusca 1(7):47–48. Type species: *Strombus canarium* Linné, 1758, by original designation. Abbott attributed this taxon to Kira, 1955, whose use was a nomen nudum. See Bieler & Petit, (1996) for a discussion of the authorship of this taxon. Strombidae.

Namrutua Abbott, 1948. As a subgenus of *Hua* Chen, 1943. Bulletin of the Museum of Comparative Zoology Harvard 100(3):296–297. Type species: *Melania ningpoensis* Lea, 1856, by original designation. Thiaridae.

Pitarenus Rehder and Abbott. 1951. As a subgenus of *Pitar* Römer, 1857. Revista de la Sociedad Malacologica "Carlos de La Torre" 8(2):57. Type species: *Pitaria cordata* Schwengel, 1951, by original designation. Veneridae.

Siphovasum Rehder and Abbott. 1951. As a subgenus of *Vasum* Röding, 1798. Revista de la Sociedad Malacologica "Carlos de La Torre" 8(2):61. Type species: *Vasum (Siphovasum) latiriforme* Rehder and Abbott, 1951, by original designation. Turbinellidae.

Tectininus Clench and Abbott, 1942. As subgenus of *Echininus* Clench and Abbott, 1942. Johnsonia 1(4):4. Type species: "non umbilicated *Echininus nodulosus* (Pfeiffer, 1839)", by original designation. Littorinidae.

Texadina Abbott and Ladd, 1951. As a subgenus of *Littoridina* Eydoux and Souleyet, 1852. Journal of the Washington Academy of Science 41(10):335. Type species: *T. sphinctostoma* Abbott and Ladd, 1951, by original designation. Amnicolidae.

Species-Level Taxa

Abbreviations for repositories of type material:

AM = Australian Museum, Sydney.
AMNH = American Museum of Natural History, New York.
ANSP = The Academy of Natural Sciences of Philadelphia.
BM(NH) = British Museum (Natural History), London. [now The Natural History Museum, London]
BMH = Bishop Museum, Honolulu.
CM = Carnegie Museum, Pittsburg.
DMNH = Delaware Museum of Natural History, Wilmington.
FSM = Florida State Museum, Gainesville. [now Florida Museum of Natural History]
MCZ = Museum of Comparative Zoology, Harvard University, Cambridge.
MZUM = Museum of Zoology, University of Michigan, Ann Arbor.
NMV = National Museum of Victoria, Brisbane.
PBS = Philippine Bureau of Science, Manila.
PMUH = Poey Museum, University of Havana.
RM = Raffles Museum, Singapore.
UMML = Rosenstiel School of Marine and Atmospheric Science, University of Miami.
USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C.
UT = Institute of Marine Science, University of Texas.
WAM = Western Australian Museum, Perth.

afrobellatus, *Strombus terebellatus* Abbott, 1960. Indo-Pacific Mollusca 1(2):88, plate 61, figure 2. Holotype ANSP 214295, paratypes ANSP 211423, USNM, ANSP, Coryndon Museum 1611. Pange Island, west side of Zanzibar, Tanzania. Strombidae.

alealdei, *Nanivitrea* Jaume and Abbott, 1948. Revista de la Sociedad Malacologica "Carlos de la Torre" Habana 6(1):5–7, figures 1a-c, 4. Holotype PMUH 12178, para-

types, Jaume collection 25202, USNM 488585. Cuba. Ammicolidae.

alfredi, Turbonilla (Pyrgiscus) Abbott, 1958. Monographs of the Academy of Natural Sciences of Philadelphia 11:104–105, text-figure 5, 1a-c. Holotype ANSP 198692, paratypes ANSP 198693, Ostheimer Collection. Grand Cayman Island. Pyramidellidae.

andersoni, Phalium Abbott, 1968. New name for *Cassis (Phalium) dalli* Anderson, 1929, not *Phalium dalli* (Dickerson, 1917). Miocene, Caribbean coast of Colombia. Cassidae.

arcas, Terebra (Strioterebrum) Abbott, 1954. The Nautilus 68(2):40–41, pl. 2, figure 4. Holotype USNM 613882, paratypes, USNM 613883, ANSP 191712, Steger collection (now DMNH 104984, DMNH 118028). Arcas Cays, Campeche Bank, Mexico. Terebridae.

atlantieus, Pleurobranchus (Susania) Abbott, 1949. The Nautilus 62(3):73–78, plate 5, figures 1–10. Holotype USNM 574352, paratypes USNM 574342, ANSP 184350, MCZ 165951. Soldier Key, Biscayne Bay, Florida. Pleurobranchidae.

aureofasciatus, Conus spurius Rehder and Abbott. 1951. Revista de la Sociedad Malacologica "Carlos de La Torre" Habana 8(2):64–65, plate 9, figs. 3, 4. Holotype USNM 597521, USNM 597522, Sennott collection, Woolsey collection. Off Dry Tortugas, Florida, in 20 fms. Conidae.

auricincta, Strombiformis Abbott, 1958. Monographs of the Academy of Natural Sciences of Philadelphia 11: 106–107, text-figure 5, 4. Holotype ANSP 198840, paratypes ANSP 199841, USNM 619550, ANSP 75855. Grand Cayman Island. Melanellidae.

austini, Conus Rehder and Abbott. 1951. Journal of the Washington Academy of Sciences 41(1):22–24, figure 7. Holotype USNM 603017, paratypes USNM 421721, USNM 603018. Dry Tortugas, Florida. Conidae.

austini, Stenothyra Abbott, 1951. Journal of the Washington Academy of Sciences 41(1):14–16, figures 1, 3–7 Holotype USNM 603669, paratypes USNM 603670, USNM 603671, USNM 603672, MCZ. Leyte, Philippines. Stenothyridae.

balesae, Acanthochitona Abbott, 1954. American Seashells. p. 318. Holotype ANSP 349331, Bonefish Key, Florida. Abbott attributed this taxon to Pilsbry, 1940, whose use was a nomen nudum. See Lyons (1988):102 for a discussion of the authorship of this taxon. Acanthochitonidae

bayeri, Olivella Abbott, 1951. The Nautilus 64(4):111–112, plate 7, figures 2a-b. Holotype USNM 595132, paratypes USNM 412871, MCZ, ANSP, UMML. Off Ajax Reef, off Elliott's Key, Lower Florida Keys. Olividae.

blandfordi, Assiminea Abbott, 1958. Proceedings of the Academy of Natural Sciences of Philadelphia 110:247–249, plate 21. Holotype USNM 615212, paratypes USNM 513820, ANSP 193360. Samar Island, Philippines. Assimineidae.

boettgeri, Assiminea Abbott, 1958. Proceedings of the Academy of Natural Sciences of Philadelphia 110:249–251, plate 15, figure 3, plate 23. Holotype USNM 615214, paratypes USNM 613828, ANSP 193370. Leyte Island, Philippines. Assimineidae.

bonnei, Indopyrgus Abbott, 1945. Occasional Papers on Mollusks 1(1):3–4, plate 1, figures 1–6, plate 2, figures 1,2. Holotype, MCZ 147474, paratypes MCZ 147475, MCZ 147476. Lake Poso, Celebes. Hydrobiidae.

boschi, Cymatium (Ranularia) Abbott and Lewis,1970. The Nautilus 83(3):86–88, figures 1–6. Holotype DMNH 22862, paratypes AMNH 139206, ANSP 188844, Bosch collection. Al Masirah Island, Oman. Ranellidae.

branhamae, Fasciolaria distans Rehder and Abbott. 1951. Revista de la Sociedad Malacologica "Carlos de La Torre" 8(2):59–60, plate 8, figs. 4,5. Holotype USNM 597513, Branham collection, Raines collection. Off Puerto Alvaro Obregon, Tabasco, Mexico. Fasciolariidae.

caribaea, Coralliophila Abbott, 1958. Monographs of the Academy of Natural Sciences of Philadelphia 11:166–67, text-figure 3, plate 1, figures g-h. Holotype ANSP 197054, paratypes ANSP 61054, (DMNH 24282 ex ANSP 61054), ANSP 194091, ANSP 29958, ANSP 36673, ANSP 196397, ANSP 29962, ANSP 29959, ANSP 190548, ANSP 197056, ANSP 197055, ANSP 195857, MCZ 133415, MCZ 38548. Vera Cruz, Mexico. Coralliophilidae.

caribaea, Cosa Abbott, 1958. Monographs of the Academy of Natural Sciences of Philadelphia 11:112–113, text-figure 6. Holotype ANSP 200064, paratype ANSP 205419. Grand Cayman Island. Philobryidae.

clarki, Stenothyra austini Abbott, 1951. Journal of the Washington Academy of Sciences 41(1):14–16, figure 2. Holotype USNM 603673, paratypes USNM 303387. Mindoro Island, Philippines. Stenothyridae.

clarki, Conus Rehder and Abbott. 1951. Journal of the Washington Academy of Sciences 41(1):22, figures 1–6. Holotype USNM 485740, paratypes USNM 488 465, MCZ. SSW of Marsh Island, Louisiana. Conidae.

cookei, Omphalotropis Abbott, 1949. Occasional Papers of the Bishop Museum 19(15):263–266, figure 1a-e. Holotype USNM 591306, paratypes MCZ 182894, BMH 212195, numerous additional paratypes at USNM, MCZ, BMH. Saipan Island, Marianas. Synceridae.

cosmani, Chicoreus Abbott and Finlay, 1979. The Nautilus 94(4):159–162, figures 1–9. Holotype USNM 783323, paratypes AMNH, ANSP, DMNH, Cosman, Finlay, and Bijur Collections. Ocho Rios, Jamaica. Muricidae.

dinagatensis, Syncera pseudoquadrasi Abbott, 1948. Bulletin of the Museum of Comparative Zoology Harvard. 100(3):284–285. Holotype MCZ 175323, paratypes MCZ 175324, USNM 485565. Panamoan, Dinagat Island, NE of Mindanao Island, Philippines. Synceridae.

eloiseae, *Acteon* Abbott. 1973. The Nautilus 87(4):91–92, figures 1–5. Holotype DMNH 27213, paratypes DMNH 67746, Bosch collection. Al Masirah Island, Oman. Acteonidae.

emipowlusi, *Oecnebra (Oecnebra)* Abbott, 1954. The Nautilus 68(2):41–42, pl. 2, figure 3. Holotype USNM 613881, paratypes, ANSP 191711, Steger collection (now DMNH). Off Fort Myers, Florida. Muricidae.

gerrardi, *Transennella* Abbott, 1958. Monographs of the Academy of Natural Sciences of Philadelphia 11:130–131, text-figure 7, plate 4, figures a-c. Holotype ANSP 199507, paratypes ANSP 199508, ANSP 199509, (DMNH 21194 ex ANSP 199509), ANSP 199506, USNM 619551, MCZ, USNM, ANSP 199510. Grand Cayman Island. Veneridae.

grandanus, *Cantharus multangulus* Abbott, 1986. The Nautilus 100(4):120–121, figure 1. Holotype USNM 859096, paratypes ANSP, AMNH, MCZ, FSM. Black Isle, St. Joseph Bay, Gulf County, Florida. Buccinidae.

guamensis, *Syncera nitida* Abbott, 1949. Occasional Papers of the Bishop Museum 19(15):273–274, figures 8a-c, 9a-c. Holotype USNM 589997, paratypes USNM 589992, MCZ 183904, BMH 212193. Banks of the Pago River, Guam Island, Marianas. Synceridae.

habei, *Assiminea habei* Abbott, 1958. Proceedings of the Academy of Natural Sciences of Philadelphia 110:251–254, plates 16–18, 25. Holotype USNM 613213, paratypes USNM 613801, ANSP 193367, USNM 613831, ANSP 193366, (DNMH 25311 ex ANSP 193366), ANSP 193368, ANSP 193369. Leyte Island, Philippines. Assimineidae.

hectori, *Phalium* Abbott, 1968. New name for *Cassis muricata* Hector, 1886, not *Cassis muricata* Menke, 1828. Miocene, New Zealand. Cassidae.

hedgpethi, *Pleurobranchaea* Abbott, 1952. Florida State University Studies 7:1–2, plate 1, figures 1–8. Holotype USNM 574607, paratype, Hedgpeth collection. Port Aransas, Texas. Pleurobranchidae.

hoffmeyeri, *Terebra (Strioterebrum)* Abbott, 1952. The Nautilus 65(3):78–80, plate 5, figures 5–9. Holotype USNM 598077, paratypes USNM 596972, MCZ, ANSP, (DMNH 24990 ex ANSP 234286), BMH, PBS, Hadley Collection. Basay Beach, Manila Bay, Luzon Island, Philippines. Terebridae.

hummi, *Polycera* Abbott, 1952. Florida State University Studies 7:3–4, plate 2, figures 1–8. Holotype, USNM 574647, paratypes USNM 574648, Humm collection. Alligator Harbor, Franklin County, Florida. Polyceridae.

indomaris, *Lambis scorpius* Abbott, 1961. Indo-Pacific Mollusca 1(3):165–166, plate, figure. Holotype ANSP 242210, paratypes ANSP 247564, ANSP 212384, ANSP 214263, ANSP 212968. Nossi-bé, Madagascar. Strombidae.

iredalei, *Strombus vomer* Abbott, 1960. New name for *Strombus australis* Gray, 1826, not *Strombus australis* Schröter, 1805. Strombidae.

keelingensis, *Succinea* Abbott, 1950. Bulletin of the Raffles Museum 22:87–90, figures 1–7. Holotype USNM 488579, paratypes, USNM 488580, RM, BM(NH). North Keeling Island, Cocos-Keeling Islands, Succineidae.

klineorum, *Strombus* Abbott, 1960. Indo-Pacific Mollusca 1(2):70, plate 20, figures 20–21. Holotype ANSP 247621, paratypes ANSP 211121, ANSP 211173, MCZ 224889. Powder Bay, Sri Lanka. Strombidae.

kurodai, *Fukuia* Abbott and Hunter, 1949. Proceedings of the Helminthological Society of Washington 16(2):80–82, plate 1, fig. 6, plate 2, fig. 4. Holotype USNM 593365, paratypes USNM 488538, USNM 488517. Takeda River, near Maruoka City, Fukui Prefecture, Honshu, Japan. Amnicolidae.

kurodai, *Phalium* Abbott, 1968. Indo-Pacific Mollusca 2(9):105–106, plate 87. Holotype NSMT, paratypes ANSP 241694. Tosa Bay, Shikoku, Japan. Cassidae.

latiriforme, *Vasum (Siphovasum)* Rehder and Abbott. 1951. Revista de la Sociedad Malacologica "Carlos de La Torre" 8(2):61–62, plate 9, figs. 5,6. Holotype USNM 597517, paratypes, USNM 597518,
Sennott collection, Raines collection. NW of Cape Catoche, Yucatan, Mexico, in 18–20 fms. Turbinellidae.

luzonica, *Assiminea habei* Abbott, 1958. Proceedings of the Academy of Natural Sciences of Philadelphia 110:254, plates 15, figure 9. Holotype ANSP 96035, paratypes ANSP 193356, ANSP 193355, USNM 201151. Luzon Island, Philippines. Assimineidae.

margaritensis, *Murex* Abbott, 1958. Monographs of the Academy of Natural Sciences of Philadelphia 11:61, plate 1, figures n-o. New name for *Murex imperialis* Swainson, 1831, not *Murex imperialis* G. Fischer, 1807. Muricidae.

marshallensis, *Assiminea nitida* Abbott, 1958. Proceedings of the Academy of Natural Sciences of Philadelphia 110:256, plate 15, figure 8. Holotype USNM 615210, paratypes USNM 580909, ANSP 193364. Japtan Island, Eniwetok Atoll, Marshall Islands. Assimineidae.

minirosea, *Oecnebra (Oecnebra)* Abbott, 1954. The Nautilus 68(2):43–44, pl. 2, figure 1. Holotype USNM 103380, paratypes, USNM 161271, USNM 103413, USNM 416653, USNM 416655, USNM 416654. Jamaica. Muricidae.

moorei, *Olivella* Abbott, 1951. The Nautilus 64(4):112–114, plate 7, figure 1a-b. Holotype USNM 595133, paratypes USNM 595134, MCZ, ANSP, UMML. Carysfort Reef, off Key Largo, Florida. Olividae.

morrisoni, *Assiminea* Abbott, 1958. Proceedings of the Academy of Natural Sciences of Philadelphia 110:259–260. Holotype USNM 615211, paratypes USNM 614191, ANSP 193357. Teteu Island, Raroia Atoll, Tuamotu Islands. Assimineidae.

multistriata, *Fukuia* Abbott and Hunter, 1949. Proceedings of the Helminthological Society of Washington 16(2): 82–83, Plate 1, fig. 5, plate 2, figs. 5 & 11. Holotype USNM 594185, paratypes USNM 488540, USNM 487383. Takefu in Kamiyama-mura, Nannjo-gun, Fukui Prefecture, Honshu, Japan. Amnicolidae.

nipponensis, *Casmaria ponderosa* Abbott, 1968. Indo-Pacific Mollusca 2(9):200, plate 14, figures 13–14. Holotype ANSP 313258, paratypes ANSP 241636, ANSP 227579, MCZ 233233. Tanabe, Wakayama Prefecture, Japan. Cassidae.

ochroglottis, *Strombus mutabilis* Abbott, 1960. Indo-Pacific Mollusca 1(2):74–75, plate 20, figures 9–10. Holotype ANSP 250187, paratypes ANSP 185466, USNM 26652a, USNM 465685, MCZ. Mauritius. Strombidae.

orrae, *Strombus urceus* Abbott, 1960. Indo-Pacific Mollusca 1(2):66–67, plate 20, figure 28; plate 41, figure 5. Holotype ANSP 247756, paratypes MCZ, ANSP 232673, ANSP 233409, ANSP 240131, ANSP 240137. Augustus Island, Western Australia. Strombidae.

ostheimerae, *Emarginula* Abbott, 1958. Monographs of the Academy of Natural Sciences of Philadelphia 11:18, plate 1, figure c. Holotype ANSP 195983, paratypes ANSP 195982, Ostheimer collection. Grand Cayman Island. Fissurellidae.

parkeri, *Ithycythara* Abbott, 1958. Monographs of the Academy of Natural Sciences of Philadelphia 11:96, text-figure 5. Holotype ANSP 198919, paratypes ANSP 209867 Grand Cayman Island. Turridae.

patae, *Conus* Abbott, 1971. The Nautilus 85(2):49–51, figures 1–6. Holotype DMNH 44097, paratypes DMNH 44096, DMNH 40595, DMNH 44095, Finlay collection. Pompano Beach, Broward County, Florida. Conidae.

pilsbryi, *Lambis crocata* Abbott, 1961. Indo-Pacific Mollusca 1(3):158–159, plate 128, figures 1–2. Holotype ANSP 156123, paratypes MCZ 49694, BMH 68268. Nuku Hiva, Marquesas. Strombidae.

pseudoquadrasi, *Syncera* Abbott, 1948. Bulletin of the Museum of Comparative Zoology Harvard. 100(3):283–284, plate 1, figs. 11–13, text fig. 12. Holotype MCZ 175325, paratypes MCZ 175326, USNM 485564. Bugo, Macajalar Bay, northern Mindanao Island, Philippines. Syncridae.

rasilistoma, *Tudicula (Tudicula)* Abbott, 1959. Indo-Pacific Mollusca 1(1):29, plate 4, figure 2, plate 10, figures A-C. Holotype NMV F18189, paratypes NMV, ANSP 227669. Tweed Heads, New South Wales, Australia. Turbinellidae.

saipanensis, *Paludinella conica* Abbott, 1949. Occasional Papers of the Bishop Museum 19(15):271. Holotype USNM 590891, paratypes MCZ 182889, USNM, MCZ, BMH. North end of Saipan Island, Marianas. Synceridae.

sallasi, *Murex (Murex) recurvirostris* Rehder and Abbott. 1951. Revista de la Sociedad Malacologica "Carlos de La Torre" 8(2):58–59, plate 9, figs. 7, 8. Holotype USNM 597515, USNM 597516, Sennott collection. 60 miles NW of Cape Catoche, Quintana Roo, Mexico, in 18–20 fms. Muricidae.

sennottorum, *Conus* Rehder and Abbott, 1951. Revista de la Sociedad Malacologica Carlos de la Torre 8(2):63, pl. 9, figures 1–2. Holotype USNM 597519, paratypes, USNM 597520, Sennott collection. SW of Campeche, Mexico. Conidae.

sphinctostoma, *Littoridina (Texadina)* Abbott and Ladd, 1951. Journal of the Washington Academy of Science 41(10):335–338. Holotype USNM 596722, paratypes, USNM 596723, USNM 596724, MCZ, ANSP 187519, MZUM, UT. N of Webb Point, NW side of San Antonio Bay, 27 miles NE of Rockport, Texas. Amnicolidae.

springeri, *Anadara* Rehder and Abbott. 1951. Revista de la Sociedad Malacologica "Carlos de La Torre" 8(2):54, plate 8, figs. 8, 9. Holotype USNM 597375, paratypes USNM 538689, USNM 603848, USNM 603843. 12 miles off Dry Tortugas, Florida, in 66–60 fms. Arcidae.

stegeri, *Terebra (Myurella) floridana* Abbott, 1954. The Nautilus 68(2):39–40, pl. 2, figures 5,6. Holotype USNM 613884, paratypes, USNM 613885, USNM 605184, ANSP 191709, Steger collection (now DMNH 105856). Off Campeche, Mexico. Terebridae.

thielei, *Assiminea* Abbott, 1958. Proceedings of the Academy of Natural Sciences of Philadelphia 110:242–244, plate 15, figure 5, plates 9, 22. Holotype USNM 609577, paratypes USNM 613802, USNM 613813, USNM 613848, USNM 1018, ANSP 193358, ANSP 193359, MCZ. Leyte Island, Philippines. Assimineidae.

transversum, *Microcardium* Rehder and Abbott. 1951. Revista de la Sociedad Malacologica "Carlos de La Torre" 8(2):56, plate 9 figs. 9, 10. Holotype USNM 485734. 50 miles SSW of Marsh Island, Louisiana, in 29 fms (Pelican station 94–1). Cardiidae.

vector, *Phalium (Semicassis)* Abbott, 1994. The Nautilus 107(3):94–96, figures 1,2. Holotype, USNM 860326, paratypes, Dan collection. Saya de Malha Bank. Cassidae.

victoriae, *Clenchiella* Abbott, 1948. The Nautilus 61(3): 76–80, plate 5, figures 1–7. Holotype USNM 488534, paratypes USNM 488535, MCZ, ANSP 183548, MZUM, CM. San Joaquin River, Leyte Island, Philippines. Amnicolidae.

virginensis, *Latirus (Polygona)* Abbott, 1958. Monographs of the Academy of Natural Sciences of Philadelphia 11:76, text-figure 4, plate 2, figure r. Holotype ANSP 196459, paratypes ANSP 34975, ANSP 34968, ANSP 34969. St. Thomas Island, Virgin Islands. Faseiolariidae.

wilsoni, *Strombus (Canarium)* Abbott, 1967. Indo-Pacific Mollusca 1(7):455–456, plate 328, figures 1–3. Holotype ANSP 253088, paratypes ANSP 212695, WAM 847–66, WAM 840–66, WAM 838–66, WAM 851–66, ANSP, BMH. Zanzibar, Tanzania. Strombidae.

winkworthi, *Phalium* Abbott, 1968. Indo-Pacific Mollusca 2(9):179–181, plates 165–168. Holotype AM, paratypes ANSP 272396, WAM 159–62. Abrolhos Islands, Western Australia. Cassidae.

zanzibarica, *Tudicula* Abbott, 1958. Notulae Naturae 305:1–4, figures 1–7. Holotype ANSP 225261, paratypes ANSP 225262, 2 additional paratypes. Ras Nungwi, Zanzibar, Tanzania. Turbinellidae.

PUBLICATIONS OF R. TUCKER ABBOTT

R. Tucker Abbott was a prolific author, including among his works numerous newspaper articles, book reviews and sound recordings. Many of his popular works were published in multiple printings and editions, some were translated and published in several languages. The various editions of his works are listed here, but individual printings are not. Many of Tucker's book reviews were published in several different journals or shell club publications. The following list of publications is arranged in chronological order. Dates of publication are provided when they could be determined. Dates of items published in publications of the United States National Museum are from Anonymous (1971), those published in *The Nautilus* are from Coan and Harasewych (1993).

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Clench, W. J. and R. T. Abbott. 1943. The Genera *Gaza* and *Livona* in the Western Atlantic. Johnsonia 1(12):1–9. [December 31]

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At the time of his death, R. Tucker Abbott was working on a number of books. Among these was our collaboration on the third edition of *American Seashells*, on which he will be a co-author.

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Petitilla, New Name for *Petitella* Wise, 1996, a Preoccupied Name (Mollusca: Gastropoda: Pyramidellidae)

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In a recent study of phylogenetic relationships within the family Pyramidellidae, I proposed the generic name *Petitella* Wise, 1996, within the new subfamily Sayellinae. The editors of *Zoological Record* have since brought to my attention that *Petitella* is preoccupied, having previously been applied to a genus of fish (Géry & Boutiére, 1964). A replacement name is therefore proposed.

Petitilla, new name for *Petitella* Wise, 1995:495, not *Petitella* Géry & Boutiére, 1964:474.

Type species, by original designation of *Petitella* Wise, 1996, *Sayella crosseana* Dall, 1885, Recent, Western Atlantic.

The new name honors Richard E. Petit for his many invaluable contributions to malacology, as did the name it replaces.

I thank the editors of Zoological Record for bringing this to my attention.

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Cenozoic Biogeographic History of the Eurythermal Genus *Retrotapes*, New Genus (Subfamily Tapetinae) from Southern South America and Antarctica

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ABSTRACT

Retrotapes, new genus, comprises a group of Neoaustral bivalves that appeared in the southern circumpolar regions by the Eocene and have since been confined to the high latitudes of the southern hemisphere. Its presence in the Tertiary strata of Antarctica and southern South America reflects an active faunal interchange between both regions during the Eocene. *Retrotapes* is here proposed to include to those Recent and Tertiary representatives of the Subfamily Tapetinae (Family Veneridae) from southern South America and Antarctica that had been previously placed in *Venus* Linné, 1758, *Marcia* H. and A. Adams, 1857, *Eurhomalea* Cossmann,1920, *Samarangia* Dall,1902, and *Kalelysia* Römer, 1857. The Argentine Tertiary species *Retrotapes ninfasiensis*, new species, *R. fuegoensis*, new species, *R. striatolamellata* (Ihering, 1897) and *R. scutata* (Ihering, 1907) are here described and illustrated. The Recent Argentine *Venus exalbida* Chemnitz, 1795 and *Venus lenticularis* Sowerby, 1835, the Antarctic *V. antaretica* Sharman and Newton, 1894 and *V. newtoni* Wilckens, 1911 (Eocene-early Oligocene?, La Meseta Formation), and the Neogene Chilean species *V. navidadis* Philippi, 1887 and *V. colchaguensis* Philippi, 1887 are also included in this new genus.

Key words: Tapetinae, *Retrotapes*, new genus, biogeography, Neoaustral, Tertiary, Argentina, Chile, Antarctica.

INTRODUCTION

The Subfamily Tapetinae (Family Veneridae) shows a moderately high degree of endemism in Recent as well as in Tertiary faunas. The known geographic distribution of most living tapetines is mainly restricted to the southern hemisphere. This subfamily is particularly abundant in the southern Indo-Pacific region, where it is represented by more than seventy species. Most of the Indo-Pacific genera, among them *Katelysia* Römer, 1857, *Marcia* H. & A. Adams, 1857, *Granicorium* Hedley, 1906, *Hemitapes* Römer, 1864, *Notirus* Finlay, 1928, *Notopaphia* Oliver, 1923, *Eumarcia* Iredale, 1924, *Paphirus* Finlay, 1927, and *Gomphinella* Marwick, 1927, are restricted to New Zealand and Australia. Others, including *Gomphina* Mörch, 1853, *Venerupsis* Lamarck, 1818, *Ruditapes* Chiamenti, 1900, *Tapes* Mergele von Mühlfeld, 1811, and *Paphia* Röding, 1798, are also found beyond those regions.

In contrast, Recent tapetines are poorly represented in the littoral zones along both coasts of the American continents. The subfamily is known from only twelve living North American species distributed among the genera *Ruditapes*, *Liocyma* Dall, 1870, *Psephidia* Dall, 1902 and *Irus* Schmidt, 1818, as well as five South American taxa assigned to the genera *Eurhomalea* Cossmann, 1920 and *Retrotapes*, new genus.

The fossil record in the Americas reveals that Tapetinae were more abundant in the Tertiary than in the Recent fauna. Two diverse and different assemblages appeared during the Tertiary, one restricted to North America, the another to austral latitudes. The northern assemblage comprises the endemic genera *Liocyma*, *Cyclorisma* Dall, 1902, *Psephidia* and *Sinonia* Stephenson, 1952, as well as taxa with european affinities such as *Mercimonia* Dall, 1902, *Flaventia* Jukes-Browne, 1908, *Paraesa* Casey, 1952 , *Legumen* Conrad, 1858 and *Textivenus* Cossmann, 1886. The less diverse austral assemblage, characterized by *Eumarcia*, *Katelysia*, *Atamarcia* Marwick, 1927 and *Retrotapes*, appeared during the early Tertiary in the southernmost region of South America and Antarctica.

Figure 1. Stratigraphic distribution of *Retrotapes*, new genus, in South America and Antarctica.

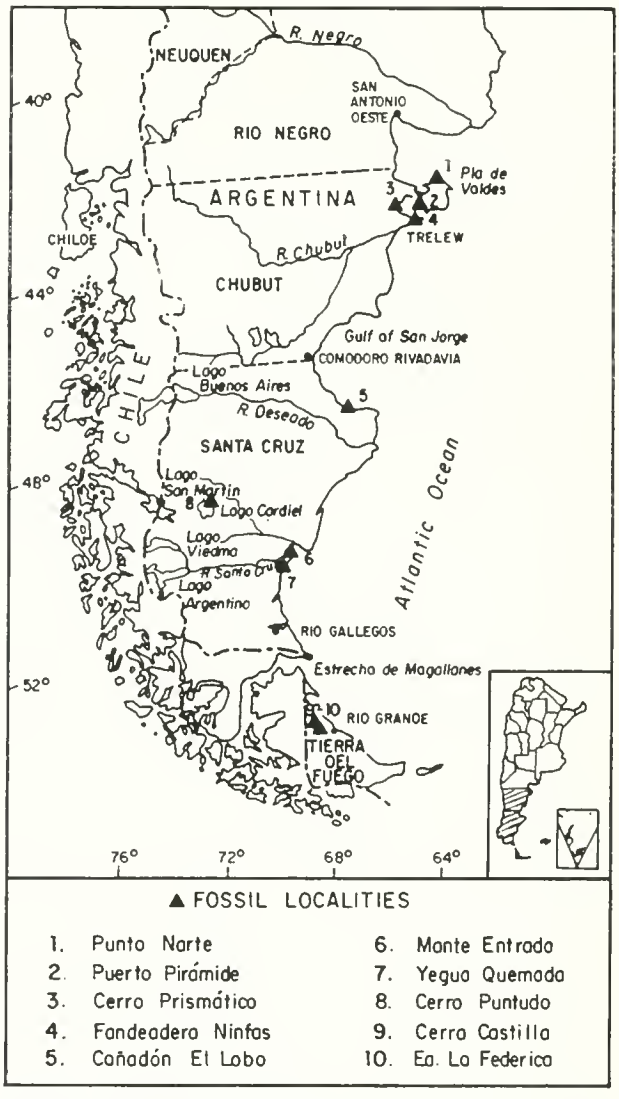


Figure 2. Geographic distribution of fossil localities referred to in this paper.

The species that are here included in *Retrotapes* occur in the Tertiary rocks of Chile, Antarctica and Argentina, and are at present distributed in the littoral zones along both coasts of South America (Figure 1), where they are represented by *R. lenticularis* (Sowerby, 1835) and *R. exalbida* (Chemnitz, 1795).

This paper includes the systematic description of the Tertiary Argentine representatives of *Retrotapes*: *R. ninfasiensis* new species (Puerto Madryn Formation, middle Miocene), *R. fuegoensis* new species (Carmen Silva Formation, late Oligocene-early Miocene), *R. striatolamellata* (Ihering, 1897) (Monte Léon Formation, late Oligocene-early Miocene) and El Chacay Formation (late Eocene) and *R. scutata* (Ihering, 1907) (San Julián Formation, late Eocene). *Venus antarctica* Sharman and Newton, 1894 and *V. newtoni* Wilekens, 1911 from the Eocene-early Oligocene? La Meseta Formation (Antarctica), and the Chilean species *V. navidadis* Philippi, 1887 (early Miocene), *V. colchaguensis* Philippi, 1887 (early Miocene-Pliocene) and *V. lenticularis* (Pliocene-Holocene), along with the Recent *V. exalbida*, are also placed in *Retrotapes*.

MATERIAL AND METHODS

The fossil material reported here came from the thick, marine, sedimentary, Tertiary sequence exposed along the eastern coast of Patagonia from San Antonio Oeste (Río Negro Province), southward to Isla Grande of Tierra del Fuego, and at Cerro Puntudo (Lago Cardiel), a locality situated in the western region of Patagonia (Santa Cruz Province) (Figure 2). Lithostratigraphic units yielding representatives of *Retrotapes* are the Puerto Madryn Formation (Haller, 1978), the Monte León Formation (Bertels, 1970), the Carmen Silva Formation (Codignotto & Malumián, 1981), the San Julián Formation (Bertels,

1970) and the El Chacay Formation (Chiesa & Camacho, 1984).

The Puerto Madryn Formation, exposed at Peninsula Valdés (Chubut Province), is believed to represent one of the youngest Tertiary marine units recognized in Patagonia, having been reported by del Río (1988, 1992) as being of middle Miocene age. This formation consists of 150 meter thick, whitish cinerites and yellowish sandstones alternating with highly fossiliferous calcareous sandstones and muddy or sandy shelly beds. *Retrotapes* is abundant at the basal ochreous shelly sandstones that are exposed at Cerro Prismático (horizon N 2, del Río, 1992), where it is associated with "*Chlamys*" *actinodes* (Sowerby, 1846), *Purpurocardia leonensis* del Río,1986, *Glycymerita magna* del Río, 1992, *Aequipecten paranensis* (d'Orbigny, 1842), *Dosinia meridionalis* (Ihering, 1897) as well as with the gastropod *Valdesia valdesiensis* del Río, 1985. *Retrotapes* is less common in the gray, massive, fine sandstones that comprise the base of the section at Punta Norte (horizon PN 2, del Río, 1992), where articulated specimens have been found in life positions along with *Anadara (Rasia) lirata* (Philippi, 1893), *Glycymeris longioriformis* del Río, 1992, *Lucinisa* sp., "*Cyclocardia*" *nortensis* del Río, 1986, *Dosinia meridionalis* (Ihering, 1897), *Dosinia cuspidata* del Río, 1994, *Ameghinomya meridionalis* (Sowerby, 1846) and *A. argentina* (Ihering, 1897). *Retrotapes* also occurs in the strata placed at the top of the sequence exposed at Punta Ninfas (horizon F 9, del Río, 1992) and is associated with *Glycymerita magna* del Río, 1992, *Amusium paris* del Río, 1992, and *Aequipecten paranensis* (d'Orbigny, 1842).

Retrotapes has also been collected from exposures of the late Oligocene Monte León Formation that crop out at the mouth of the Santa Cruz River (Santa Cruz Province). Here it is locally abundant in the highly fossiliferous, coquinoid sandstones situated 80 meters above sea level at Monte Entrada and in the sandy lenses present at the sea cliffs at Las Cuevas. Fossil material is well preserved at both localities where disarticulated valves are associated with a rich bivalve fauna characterized by *Cucullaea alta* (Sowerby, 1846), *Neilo ornata* (Sowerby, 1846), *Pecten proximus* Ihering, 1897, *Venericardia inaequalis* Philippi, 1887, *Limopsis insolita* Sowerby, 1846, *Australocallista iheringii* (Cossmann,1898), *Dosinia meridionalis* Ihering, 1897, *Perna quadrisulcata* Ihering, 1897 and *Phacoides crucialis* Ihering,1907.

Specimens of *Retrotapes* found at the Carmen Silva Formation (late Oligocene-early Miocene) occur in pebbly shelly sandstones at the top of the sequence that crops out at Cerro Castillo and Estancia La Federica. Material is abundant and well preserved, with most of the specimens consisting of articulated valves.

Material coming from the San Julián Formation was collected by C. Ameghino from sedimentary marine outcrops at Cañadón El Lobo (= Cañadón Tournöuer), close to Punta Casamayor. The age of the San Julián Formation is still debated, ranging from late Eocene to early Oligocene (Nañez, 1988; Camacho, 1984, 1995), as recently documented by del Río (1995). Only one fairly well-preserved valve of *Retrotapes* is known from the uppermost, highly-fossiliferous, orange coquinoid sandstones that alternate with green or yellowish gray silstones and sandstones exposed at Cañadón El Lobo.

Retrotapes is poorly represented in the El Chacay Formation, exposed at Cerro Puntudo (Lago Cardiel). Chiesa and Camacho (1994) placed this unit in the late Eocene based on biostratigraphic correlations with the San Julián Formation.

Specimens described in this paper are housed in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires, Argentina, in the Centro de Investigaciones en Recursos Geológicos (CIRGEO-PI), Buenos Aires, Argentina, Facultad de Ciencias Exactas y Naturales of the Universidad de Buenos Aires (CPBA), Buenos Aires, Argentina, Dirección Nacional Servicio Geológico (DNSG), Buenos Aires, Argentina and in the Department of Earth and Atmospheric Science, Purdue University (PU), Indiana, USA.

SYSTEMATIC PALEONTOLOGY

Phylum MOLLUSCA Linné, 1758
Class BIVALVIA Linné, 1758
Subclass HETERODONTA Neumayr, 1884
Order VENEROIDA H. & A. Adams, 1856
Superfamily VENEROIDEA Rafinesque, 1815
Family VENERIDAE Rafinesque, 1815
Subfamily TAPETINAE H. & A. Adams, 1857

Diagnosis: Members of this subfamily are characterized by having smooth inner ventral margins and three cardinal teeth in each valve, with at least two of them grooved or bifid. Most Tapetinae have exterior surfaces with commarginal lines and/or grooves, while others have polished surfaces or very fine radial threads. Though no attention has been paid to the presence of a lunule or the arrangement of cardinal teeth, these characters, along with the general outline of the cardinal platform, are of taxonomic importance at the generic level. When present, and viewed dorsally, the lunule may be concave or convex, and is limited by a groove and/or ridge that is distinguished from the remaining surface of the shell by its different ornamentation, or by the presence of a groove.

Hinge characters have proven to be the most useful morphological feature for distinguishing among genera. Cardinal teeth may be placed on a thin, slender, cardinal platform with a straight ventral margin, or situated on a short, broad, strongly arcuate platform. While some genera are characterized by having teeth that diverge from a point situated below the beaks, others have non-divergent teeth (Figure 3). Divergent teeth are characterized by a strongly forward-inclined anterior tooth, a vertical median tooth, and a backward-inclined posterior tooth. Genera with non-divergent teeth may have three cardinal teeth sloping backwards (posterior tooth nearly

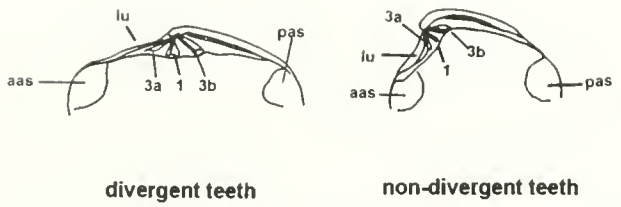


Figure 3. Hinge teeth types in Tapetinae. aas, anterior adductor muscle scar; lu, lunule; pas, posterior adductor muscle scar; 1,3a,3b, cardinal teeth.

horizontal) or have the median and posterior teeth inclining backwards, with the anterior tooth being vertical.

Genus *Retrotapes*, new genus

Patagomalea del Río, 1991:93, nomen nudum.

Diagnosis: Shell large to medium sized, highly variable in outline. Escutcheon facing opposite valve, usually wider, smoother on left valve than on right in adults. Lunule large to medium sized, deeply impressed, strongly differentiated from remaining shell surface, highly to moderately concave, nearly vertical, with longitudinal median sulcus, bounded by deep lunular groove. Hinge heavy, short, arcuate behind teeth, with three long cardinal teeth. Right and left posterior teeth nearly horizontal in some species, left and right anterior teeth nearly vertical to strongly sloping backwards, nearly paralell to posterior teeth; left median tooth, right median and posterior teeth bifid or grooved.

Type species: *Retrotapes ninfasiensis*, new species.

Type locality: Valdés Peninsula, Chubut Province, Argentina, Puerto Madryn Formation (Middle Miocene).

Stratigraphie range: Eocene to Holocene, southern South America and Antarctica.

Etymology: *retro-* L. backwards. Referring to the inclination of non-divergent cardinal teeth towards the posterior region of the shell.

Remarks: Recent as well as fossil species belonging to *Retrotapes* have previously been placed in *Venus* Linné, 1758, (Philippi, 1887; Ihering, 1897), in *Marcia* (Dall, 1902; Ihering, 1907; Riveros & Gonzalez, 1950), in *Samarangia* Dall, 1902 (Jukes-Browne, 1908; Carcelles, 1944; Carcelles & Williamson, 1951; Castellanos, 1970; Rios, 1975) in *Eurhomalea* (Keen, 1954; Soot-Ryen, 1959; Ramorino, 1968; Fisher-Piette & Vukadinovic, 1977; Malumián *et al.* 1978, Zinsmeister, 1984; Stilwell & Zinsmeister, 1992) and in *Katelysia* (Dall, 1902; Jukes-Browne, 1908; Riveros & Gonzalez, 1950).

The taxonomic placement of the Holocene South American species *Venus exalbida* (Figures 22–23, 41) and *Venus lenticularis* (Figures 19–21), here assigned to *Retrotapes*, has long been debated, and the phylogenetical relationships of these species within the family Veneridae were misunderstood. Dall (1902) incorrectly interpreted Fischer's (1887) statement about *V. exalbida* being the type species of the genus *Marcia*, considered *Samarangia* (type species *Venus quadrangularis* Adams & Reeve, 1850) to be a section of *Marcia*, and placed *V. lenticularis* in *Samarangia*. He thought *V. exalbida*, *V. lenticularis* and *V. quadrangularis* to be part of a closely related group of species related to *Marcia*. Jukes-Browne

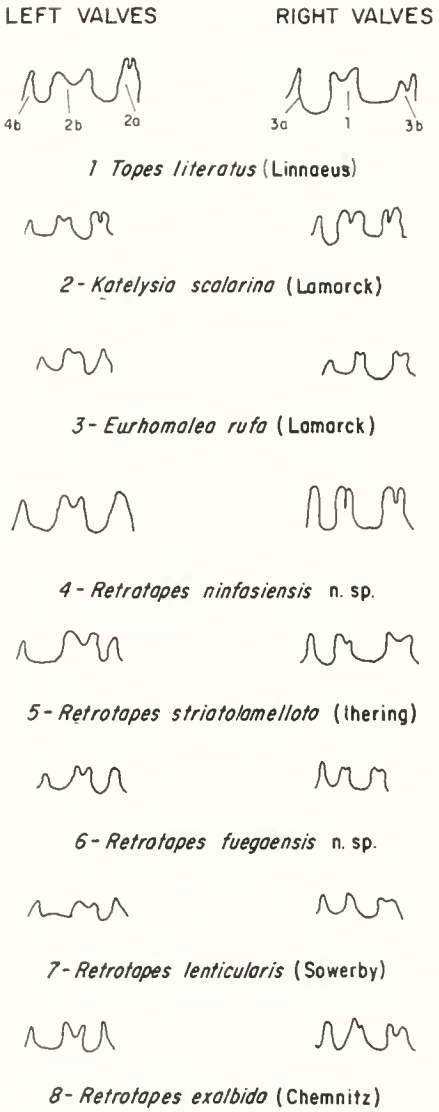
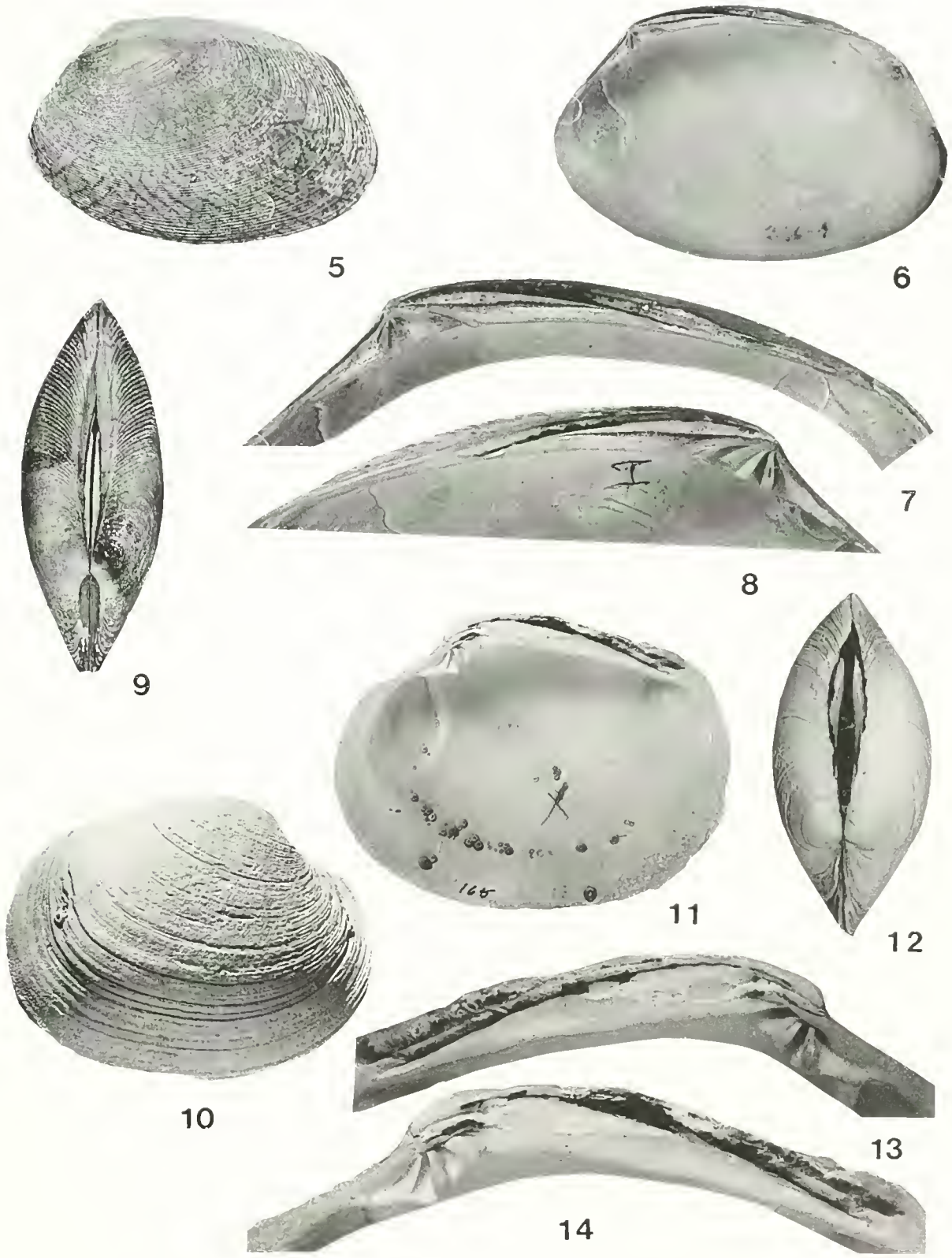


Figure 4. Schematic cross-sections of hinge teeth. *Tapes literatus* (Linné). MACN 266–1, Indian Ocean, Recent (2.4×); *Katelysia scalarina* (Lamarck). PU 863–5, Victoria, Australia. Recent (2.4×); *Eurhomalea rufa* (Lamarck). PU 165, Chile, Recent. (1.2×); *Retrotapes ninfasiensis*. new species. CPBA 15.110, Fondeadero Ninfas, middle Miocene, Puerto Madryn Formation, Argentina (1.2×); *Retrotapes striatolamellata* (Ihering). MACN 2639, Yegua Quemada, late Oligocene, Monte León Formation, Argentina (1.2×); *Retrotapes fuegoensis*, new species. PU 355–12, Cerro Castillo, late Oligocene-early Miocene, Carmen Silva Formation, Argentina (1.2×); *Retrotapes lenticularis* (Sowerby). PU 165, Chile, Recent (1.2×); *Retrotapes exalbida* (Chemnitz) MACN 21.172, Argentina, Recent (1.2×).



Figures 5–9. *Tapes literatus* (Linné). MACN 266–1, Indian Ocean, Recent. **5.** Exterior view of left valve (1×). **6.** Interior view of right valve (1×). Enlargements of **7.** right and **8.** left hinges (2×). **9.** Dorsal view of an articulated specimen (1×). **Figures 10–14.** *Eurhomalea rufa* (Lamarck). PU 165, Chile, Recent. **10.** Exterior and **11.** interior views of right valve (1×). **12.** Dorsal view of an articulated specimen (1×). Enlargement of **13.** left and **14.** right hinges (2×).

(1908) designated *Venus pinguis* Chemnitz, 1782 (= *V. opima* Gmelin, 1791) as the type species of *Marcia*, and excluded *V. exalbida* from this genus.

Venus quadrangularis (see Fischer-Piette & Vukadinovic, 1977:22, figs.207–211, for illustrations of the species) cannot be related to either *V. exalbida* or *V. lenticularis* because of the presence in *V. quadrangularis* of a smooth exterior surface, a pustular left anterior lateral tooth and an entire pallial line, characters that allowed Keen (1969) to segregate *Samarangia* in the Subfamily Samarangiinae. Other diagnostic features, including the hinge and lunular characteristics of *V. exalbida*, *V. lenticularis*, as well as those of their Tertiary ancestors, require the erection of the new genus *Retrotapes*. It is placed in the Subfamily Tapetinae on the basis of the presence of shells with a smooth inner ventral margin, moderate to very deep pallial sinus, three cardinal teeth in each valve with two of them deeply grooved or bifid, and the absense of lateral teeth. Morphological features that distinguish *Retrotapes* from the remaining genera of the subfamily are the presence of non-divergent cardinal teeth and a well defined, concave lunule, bounded by a deep lunular groove and ridge.

Eurhomalea, represented by its type species *E. rufa* (Lamarck, 1818) (Figures 4, 10–14) and by *E. salinensis* Ramorino, 1968 (see Ramorino, 1968:218, pl.3, fig.2, pl.9, figs.2–3 for illustrations of the type species), is distributed along the Peruvian and Chilean coasts and has recently been placed in the Subfamily Chioninae (Fischer-Piette & Vukadinovic, 1977). However, the presence of a smooth inner ventral margin in *Eurhomalea* indicates that it is more accurately assigned to the Subfamily Tapetinae. It clearly differs from *Retrotapes* in lacking both lunule and escutcheon, in having a straight dorsal margin, a more antero-posteriorly elongate shell, and a narrower hinge plate than *Retrotapes*. Moreover, the cardinal teeth are markedly smaller than those of *Retrotapes* and quite divergent from a point situated below the beaks. The anterior cardinal teeth of both valves in *Eurhomalea* slope forward. The left posterior and right anterior cardinal teeth are much lower than in *Retrotapes*, and the left middle, and right posterior and middle teeth are only shallowly grooved.

Katelysia (type species: *Venus scalarina* Lamarck, 1818) (Figures 4, 25–28), a middle Miocene-Holocene genus confined to New Zealand and Australia, differs in having a different outline, a narrower lunule and escutcheon, a shallower pallial sinus, and a shorter cardinal teeth than *Retrotapes*.

Marcia opima, the Indo-Pacific type species of *Marcia*, was illustrated by Abbott and Dance (1986:363). The genus differs from *Retrotapes* in having a smooth exterior shell surface, a high umbonal area, a weakly defined escutcheon, and a nearly smooth and lightly impressed lunule that lacks a lunular groove. These genera may also be separated because *Marcia* has lower, narrower and more widely divergent teeth than *Retrotapes* with the anterior cardinal teeth inclining forward.

Eumarcia (type species *Venus fumigata* Sowerby, 1853, illustrated by Lamprell & Whitehead, 1992, pl.74, fig.589; Abbott & Dance, 1986:363) a common genus in New Zealand and Australia, is easily separated from *Retrotapes* on the basis of its oval and smooth shells, a lunule that is not impressed and that is bounded by a weak line, divergent teeth with left anterior and middle cardinal teeth deeply grooved and equal in size, and in having a left posterior tooth that is fused to nymph.

The Tertiary New Zealand *Atamarcia* (type species *Eumarcia suleifera* Marwick, 1927, figs.200, 203, 205, early Oligocene-late Pliocene) differs from *Retrotapes* in being sculptured with commarginal grooves, in having a fairly impressed lunule, with a shallow lunular groove, divergent teeth with curved posterior teeth, and with the left anterior and middle teeth being of equal width.

The monotypic, lower Pliocene *Opimarcia* Marwick, 1948, (type species: *O. healyi* Marwick, 1948, pl.5, figs.1, 2, 4) is distinguished from *Retrotapes* in having oval, inflated shells, very prominent beaks, a poorly defined lunule not bounded by a lunular groove, a fairly well-developed escutcheon, fine irregular commarginal ridges on the posterior and anterior ends of valves, a shorter pallial sinus than *Retrotapes*, and divergent teeth with a strongly curved right posterior tooth and a triangular, deeply grooved left anterior tooth.

Tapes (type species: *Venus literatus* Linné, 1758) (Figures 4–9) has shells that are more antero-posteriorly elongated than those of *Retrotapes*, and have a straight, horizontal dorsal margin, acuminate anterior margin, a rounded pallial sinus, straight or slightly arcuate hinge margin and a grooved left anterior cardinal tooth.

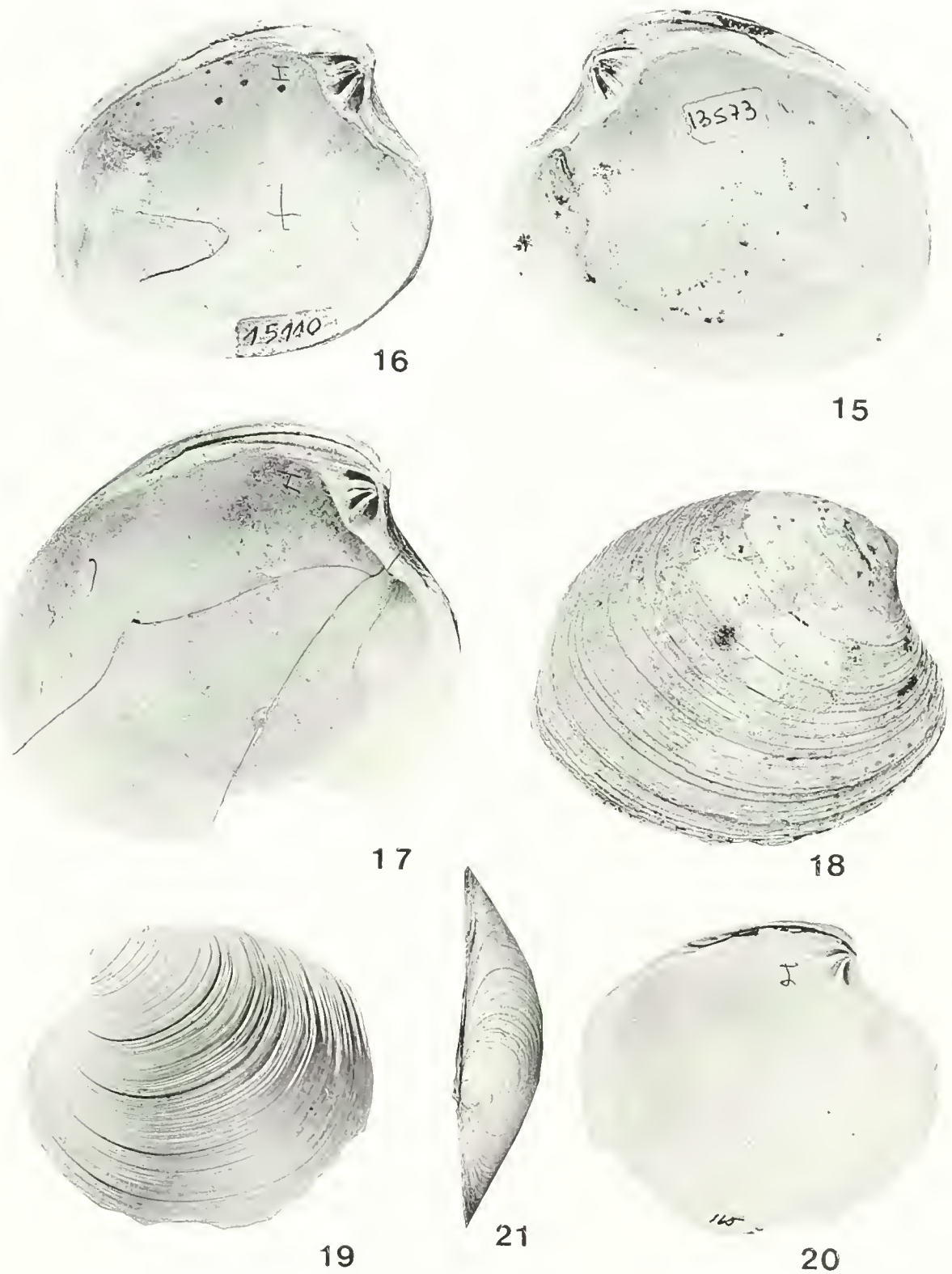
The oldest presently known record of *Retrotapes* dates to the late Eocene. This genus occurs in the San Julián Formation and the El Chacay Formation (Argentina), where is represented by *R. scutata* and *R. striatolamellata*, and in the lower and middle sections of the La Meseta Formation (late Eocene-Oligocene?, Antaretica) where *R. antarctica* and *R. newtoni* have been found.

Retrotapes ninfasiensis, new species
Figures 15–18, 40

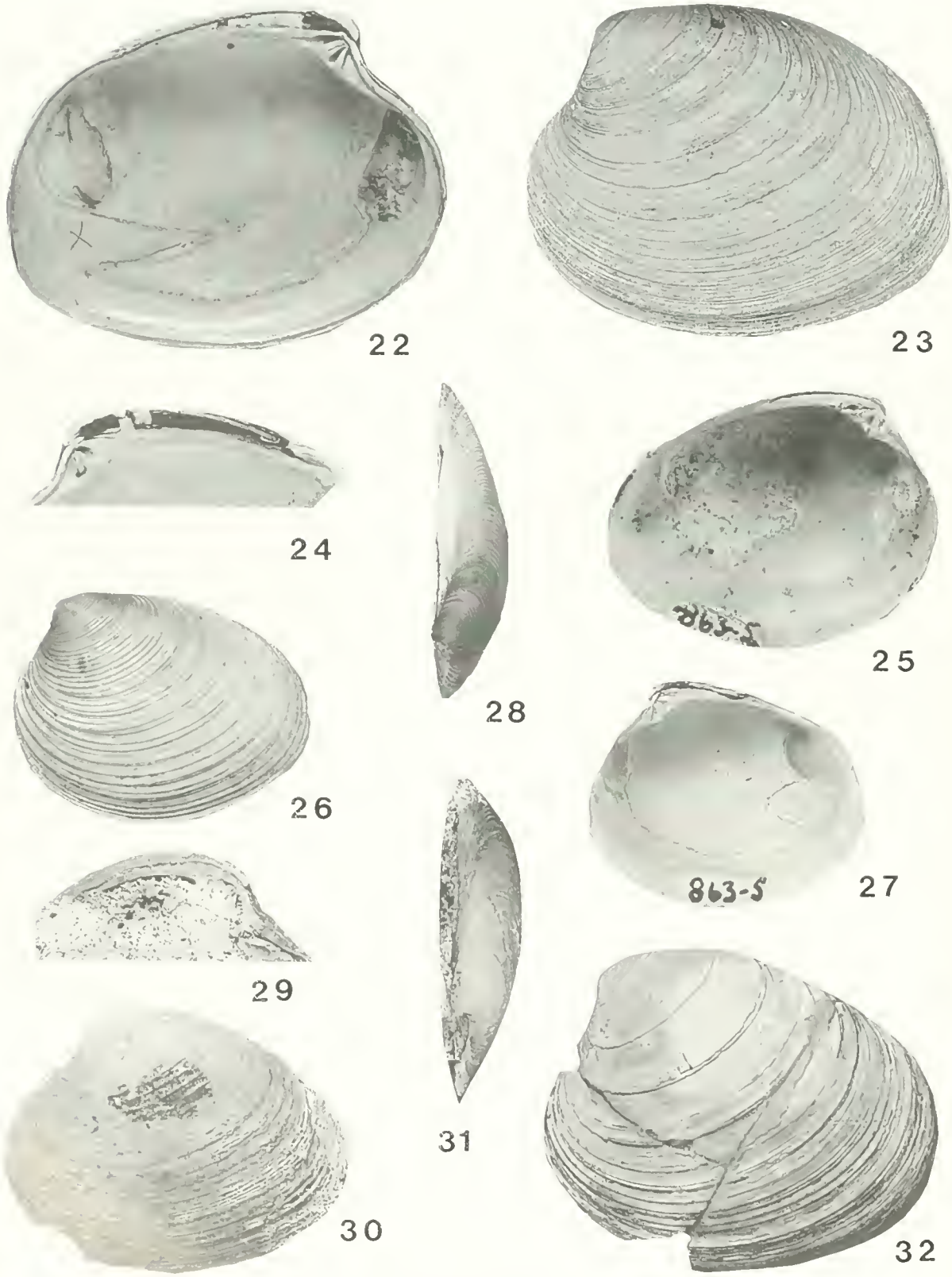
Marcia striatolamellata Frenguelli, 1926, not *M. striatolamellata* Ihering, 1897.

Diagnosis: Shell thick, ovate to subrectangular. Lunule deeply concave, nearly vertical, strongly inclined toward opposite valve. Cardinal teeth straight, high, long, thick. Median and anterior teeth sloping backwards, posterior cardinal teeth horizontal. Pallial sinus triangular, moderately short.

Description: Shell thick, large, ovate to subrectangular, weakly convex, ranging from longer than high to nearly equidimensional. Umbones small, at anterior quarter of length. Dorsal margin moderately to strongly convex, posterior margin truncated to weakly convex, ventral margin nearly straight to weakly convex, anterior margin convex. Lunule concave, with longitudinal median lunular groove, nearly vertical, strongly inclined toward opposite valve, bounded by deep groove and well marked



Figures 15–18. *Retrotapes ninfasiensis*, new species Puerto Madryn Formation, middle Miocene. **15.** Interior and **18.** exterior views of right valve of holotype, CPBA 13.573, Cerro Prismático. **16.** Interior view of left valve of paratype, CPBA 15.110, Fondeadero Ninfas. **17.** Interior view of left valve of paratype, CPBA 15.090, Punta Norte **Figures 19–21.** *Retrotapes lenticularis* (Sowerby), PU 165, Chile, Recent. **19.** Exterior, **20.** interior and **21.** dorsal views of left valve. All figures 1×



Figures 22–24. *Retrotapes exalbida* (Chemnitz) MACN 21 172, San Matías Gulf, Argentina, Recent. All figures 1×. **22.** Interior and **23.** exterior views of left valve. **24.** View of right hinge. **Figures 25–28.** *Katelysia scalarina* (Lamarck), PU 865–5, Victoria, Australia, Recent. All figures 2×. **25.** Interior, **26.** exterior, and **28.** dorsal views of left valve. **27.** Interior view of right valve.

ridge. Escutcheon on left valve wide, long, inclining toward right valve and only slightly sculptured with fine commarginal ridges; escutcheon on right valve poorly differentiated and ornamentated as remaining shell surface. Hinge short, narrow, strongly arcuate behind teeth, with three high, thick cardinal teeth per valve (Figure 4). Anterior and median teeth strongly inclined backwards, posterior teeth nearly horizontal. Right valve with deeply grooved posterior tooth separated from nymph by socket, followed by ridge, median cardinal bifid with lamellar posterior section, anterior tooth thick, equal in height to median tooth; socket for left median tooth with radial lamella. Left hinge with strong, smooth, anterior tooth, median tooth deeply grooved, with both parts equal in size, lower than anterior tooth. Posterior tooth lamellar, slightly arched, with superimposed ridge on posterior face, separated from nymph by shallow groove. Anterior adductor muscle scar oval, more deeply impressed, larger than posterior muscle scar; anterior pedal retractor muscle scar small, deeply excavated, placed above adductor. Pallial sinus relatively short, triangular, with horizontal dorsal margin, straight, ascending ventral margin; apex pointed. Exterior ornamented with widely-spaced, thin, lamellar commarginal ridges, much more numerous near ventral margin; interspaces sculptured with very fine radial threads.

Material examined: Holotype, CPBA 13.573, right valve, Cerro Primático, height 66.6 mm, length 76.2 mm. Paratypes, CPBA 15.090, left valve, Punta Norte, height 77.1 mm, length 81.9 mm, CPBA 15.110, left valve, Fondeadero Ninfas height: 60,0 mm, length: 66,0 mm; 19 left valves, 16 right valves, one articulated specimen, Punta Norte (PN 2): CPBA 15.087–15.089, CPBA 13.287-13.288, Fondeadero Ninfas (F 9): CPBA 12.345, CPBA 15.1 1 0, Cerro Prismático (N 2): CPBA 12.501, CPBA 11.646–11.650, CPBA 12.343, CPBA 12.502, CPBA 13.572, 13.574–13.575 (del Río collection)

Stratigraphic and geographic distribution: Puerto Madryn Formation, middle Miocene. Valdés Peninsula, Chubut Province.

Remarks: Specimens of *Retrotapes ninfasiensis* have erroneously been attributed to *Marcia striatolamellata* (Frenguelli, 1926), a closely related, late Oligocene species that occurs in the Monte León Formation of Santa Cruz Province. *Retrotapes striatolamellata* (Figures 33, 37–39, 42–47) may be differentiated by its longer, more convex shells, straighter dorsal margin, a lunule that is more concave and not inclined toward the opposite valve, less prominent teeth, a left anterior cardinal tooth that is less inclined backwards, being slightly arched forwards in most specimens and higher or equal in height than the median cardinal (Figure 4), and a pallial sinus that is tongue-like and longer than in *R. ninfasiensis*. *Retrotapes antarctica* (Sharman & Newton,1894, fig.3), from the La Meseta Formation (Antarctica, Eocene- early Oligocene?), differs in having a trigonally suboval outline with the dorsal margin strongly sloping backwards and rounding to the posterior margin, by the presence of a shallowly concave, narrower lunule not inclined toward the opposite valve, and a narrower, shorter pallial sinus than *R. ninfasiensis*. Moreover, *R. antarctica* has narrower teeth than *R. ninfasiensis*, the right anterior tooth inclines forwards, the left anterior tooth is grooved and higher than the median one, and the left median tooth is deeply grooved, with both sections equal in width. *Retrotapes ninfasiensis* is easily separated from *R. navidadis* (Philippi, 1887, pl.14, fig.4, Navidad Formation) because the Chilean Miocene species has a thinner and smaller shell with an acuminate anterior margin, straighter dorsal margin, more prominent beaks and a narrower lunule that is not inclined to the opposite valve. Cardinal teeth of *R. navidadis* are narrower and much shorter than in *R. ninfasiensis*, the right anterior cardinal tooth is vertical, but its anterior face inclines forward, while the left anterior cardinal tooth is lightly curved and also slopes forward. *Retrotapes lenticularis* (Sowerby) (Riveros & Gonzalez, 1950:fig.30) (Figure 19–21), a species distributed along the Chilean litoral from Coquimbo to Valparaiso, and also present in the Pleistocene outcrops in Central Chile (Herm, 1969:pl.13, figs.1–4), has subcircular shells with straight to lightly convex dorsal margins, smaller lunules not inclined toward the opposite valve, and much narrower and shallower grooved cardinal teeth than *R. ninfasiensis*. The right posterior cardinal tooth inclines backwards and is separated from the nymph by a groove, the right anterior tooth varies from being vertical to slightly inclined forward, and the left anterior and median teeth are curved. The exterior surface is covered by fine commarginal ridges, widely spaced, deep commarginal grooves, and very fine radial threads.

The Recent *R. exalbida* (Castellanos, 1970:250, pl.22, figs.4–5) (Figures 22–24, 41) is characterized by subrectangular and more inflated shells, with a shallower lunule, lower and shorter cardinal teeth with a deeper, grooved, left median tooth than in *R. ninfasiensis* (Figure 4).

Retrotapes striatolamellata (Ihering, 1897)
Figures 33, 37–39, 42–47

Marcia striatolamellata Ihering, 1897:253, pl.7, fig.44, Ihering, 1907:305.
Marcia navidadis Philippi, Ortmann, 1902:141, pl.27, fig.12.
Marcia ortmanni Ihering, 1907:304

←

Figures 29–31. *Retrotapes scutata* (Ihering). All figures 2×. Holotype MACN 429, Cañadón El Lobo, San Julián Formation, late Eocene. **29.** Left hinge, **30.** exterior and **31.** dorsal views of left valve. **Figure 32.** *Retrotapes fuegoensis*, new species 1×. Exterior view of left valve of holotype, PU 356–12, Cerro Castillo, Carmen Silva Formation, late Oligocene-early Miocene.

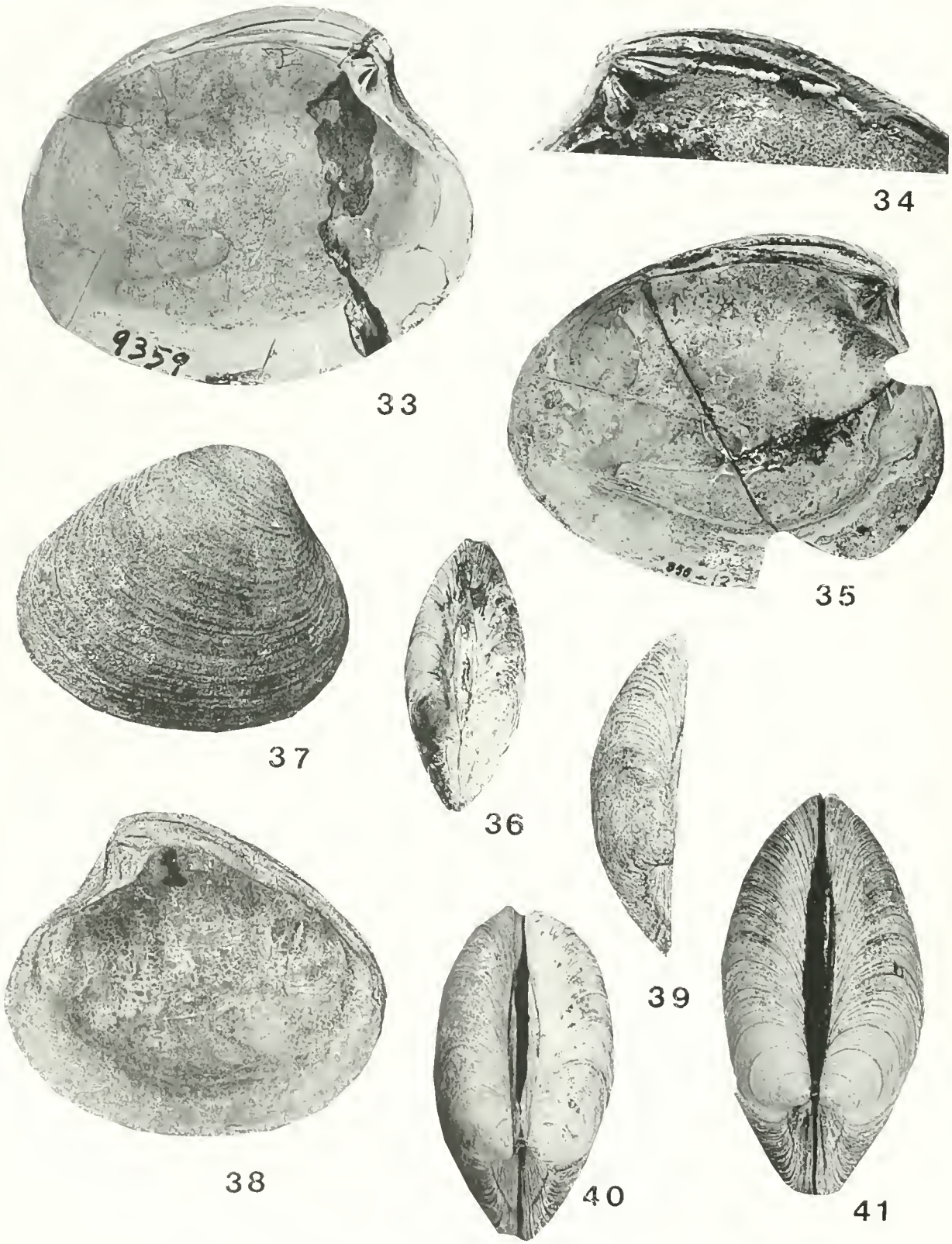


Figure 33. *Retrotapes striatolamellata* (Ihering) Interior view of left valve, CPBA 9359, Monte Entrada, Monte León Formation, late Oligocene (1×). **Figures 34–36.** *Retrotapes fuegoensis*, new species, Carmen Silva Formation, late Oligocene-early Miocene. **34.** Enlargement of right hinge, DNSG 16.500, Estancia La Federica (2×), **35.** Interior view of left valve of holotype PU 356-12, Cerro Castillo (1×) **36.** Dorsal view of an articulated paratype DNSG 16.501, Estancia La Federica (1×). **Figures 37–39.** *Retrotapes*

Diagnosis: Shell thick, ovate to subrectangular in outline, longer, more convex than *R. ninfasiensis*. Lunule strongly concave, not inclined toward opposite valve. Left anterior tooth arched (in most specimens), equal in height to median cardinal. Pallial sinus tongue-shaped, longer than in *R. ninfasiensis*.

Description: Shell thick, large, ovate to subrectangular, moderately convex, longer than high. Umbones small, at anterior quarter of length. Dorsal and anterior margins convex, ventral margin slightly convex, posterior margin slightly convex to subtruncated. Lunule broad, deeply concave, nearly vertical, not inclined toward opposite valve, marked by deep groove and distinctive ridge; longitudinal, median, lunular groove impressed. Escutcheon on left valve better defined than on right, consisting of wide, flat surface facing opposite valve, sculptured with very faint commarginal ridges. Escutcheon on right valve narrower than on left, heavily ornamented like remaining valve surface. Hinge with three narrow cardinal teeth; right valve with cardinal sloping backwards, lamellar anterior tooth, median cardinal narrowly and shallowly grooved, as high as or higher than anterior tooth. Posterior tooth broadly grooved, separated from nymph by ridge; anterior tooth of left hinge lamellar, arched, vertically or slightly inclined backwards, median tooth deeply grooved, broad, as high as, or higher than anterior tooth, narrow, straight or arched posterior cardinal tooth. Muscle adductor scars equal in size, shallowly impressed Pallial sinus deep, tongue-shaped. Commarginal sculpture of thin lamellar ridges, much more closely spaced near ventral margin. Interspaces smooth, except for growth lines.

Material examined: Holotype, MACN 437, right valve, Yegua Quemada, height 67.5 mm, length 79.3 mm; Paratypes, two left valves, Yegua Quemada, MACN 2639, height 65.0 mm, length 68.0 mm, and MACN 2640, height 65.0 mm, length 68.0 mm; two left and two right valves from Monte Entrada, CPBA 9.359, PU429, Las Cuevas, CPBA 9.391, and from Cerro Puntudo (Lago Cardiel) CIRGEO-Pl 2.513. (Ihering, Ortmann, Medina and Camacho collections)

Stratigraphic and geographic distribution: Monte León Formation (late Oligocene), from the mouth of the Santa Cruz River to Yegua Quemada, and El Chacay Formation (late Eocene), Cerro Puntudo (Lago Cardiel).

Remarks: *Retrotapes striatolamellata* comes from outcrops of the Monte León Formation at Monte Entrada, Las Cuevas and Yegua Quemada (Figure 2). This species has also been recorded from exposures of the El Chacay Formation at Cerro Puntudo (Lago Cardiel) (Santa Cruz Province). The type material of *R. striatolamellata* had been collected by Carlos Ameghino at Yegua Quemada, but this fossiliferous locality has never been recognized by subsequent authors. Ortmann (1902) placed *R. striatolamellata* in synonymy with *R. navidadis* (Philippi, 1887). Ihering (1907) considered Ortmann's specimens to represent a new taxon that he named *Marcia ortmanni* Ihering, 1907. However, a re-analysis of Ortmann's material (1902, plate 27, figure 12) (Figure 47), reveals them to be young specimens of *R. striatolamellata*.

Material coming from Cerro Puntudo (Lago Cardiel) (Figures 37–39) is limited to a poorly preserved right valve with an eroded hinge. It is placed in *R. striatolamellata* because of the arrangement of teeth, shape and size of pallial sinus, characteristics of lunule, escutcheon and exterior commarginal ornamentation. The only difference between this specimen and those coming from the Monte León Formation is in the outline of the shell. While the Cerro Puntudo specimen has a narrowly convex posterior margin with an ovate-subtriangular outline, most representatives of *R. striatolamellata* from eastern Patagonia have shells with outlines ranging from subrectangular to ovate, with a broadly convex or truncated posterior margin (Figures 33, 42–46).

Retrotapes navidadis (Philippi, 1887) is distinguished from *R. striatolamellata* in having a thinner and smaller shell with a straight dorsal margin, narrower and less concave lunule, shorter and narrower teeth and more widely spaced and homogeneously distributed commarginal ridges than in *R. striatolamellata*. *Retrotapes lenticularis* has a subcircular shell with a narrower and less concave lunule, lower and more shallowly grooved teeth than in *R. striatolamellata*, a vertical right anterior tooth, right and left posterior teeth that slope backwards, and a pallial sinus with an acute apex and concave ventral margin. *Retrotapes striatolamellata* may be easily separated from *R. antarctica* (Sharman & Newton, 1894), which has a trigonally suboval shell, slightly concave lunule, narrower teeth, a right anterior tooth that is inclined forward, and a shorter and triangular pallial sinus than *R. striatolamellata*.

Retrotapes scutata (Ihering, 1907)
Figures 29–31

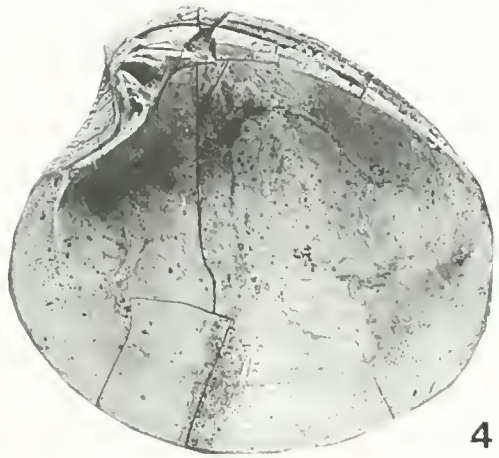
Marcia scutata Ihering, 1907:303, pl.11, fig.76.

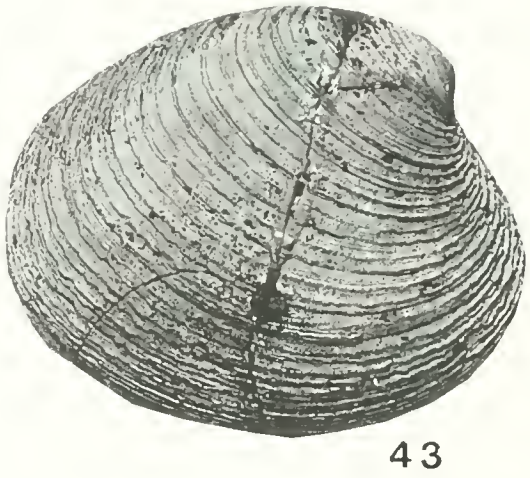
Diagnosis: Shell, elongate-oval in outline, anterior margin convex. Lunule narrow, slightly concave.

Description: Shell of medium size, elongate-oval in outline, weakly convex, longer than high. Dorsal margin

←

striatolamellata (Ihering), CIRGEO-Pl 2513 Cerro Puntudo, El Chacay Formation, late Eocene. All figures 1×. **37.** Exterior, **38.** interior and **39.** dorsal views of right valve. **Figure 40.** *Retrotapes ninfasiensis*, new species, CPBA 15.087, Punta Norte, Puerto Madryn Formation, middle Miocene. Dorsal view of articulated specimen (1×). **Figure 41.** *Retrotapes exalbida* (Chemnitz), MACN 21.172, San Matías Gulf, Argentina, Recent. Dorsal view of an articulated specimen (1×).





Figures 42–47. *Retrotapes striatolamellata* (Ihering). Monte León Formation, late Oligocene. **42.** Interior view of right valve of paratype, MACN 2639, Yegua Quemada (1×). **43.** Exterior, **44.** interior, and **46.** dorsal views of the holotype, MACN 437, Yegua Quemada (1×). **45.** Interior view of left valve of paratype, MACN 2640, Yegua Quemada (1×). **47.** P-429, Monte Entrada, interior view of left valve of juvenile specimen illustrated by Ortmann (1902.27, fig.12) (2×).

steeply sloping donwards, rounding to posterior margin; anterior margin narrowly convex. Lunule narrow, shallowly concave, not inclined toward opposite valve. Escutcheon on left valve strongly sloping toward right valve. Left hinge narrow, with lamellar anterior cardinal tooth sloping backwards, median tooth deeply grooved, posterior tooth lamellar, horizontal, slightly curved. Exterior with lamellar commarginal ridges. Interior unknown.

Material examined: Holotype, MACN 429, left valve, Cañadón El Lobo, height 32,0 mm, length 38,0 mm, (Ihering Collection).

Stratigraphic and geographic distribution: San Julián Formation (late Eocene) from Cañadón El Lobo (Santa Cruz Province).

Remarks: *Retrotapes scutata* is known only from the holotype, a left valve whose interior is unknown and the hinge partially covered with marl. The elongate-oval outline, narrow, slightly impressed lunule and thin cardinal teeth, separate this species from *R. striatolamellata* and *R. ninfasiensis*. *Retrotapes scutata* and *R. newtoni* (Wilckens, 1911: plate 1, figure 16; Zinsmeister, 1984: figure 9 I, H, K, Eocene-early Oligocene? La Meseta Formation, Antarctica), share similar features including outline, ornamentation, characters of the lunule, and arrangement of cardinal teeth. These similarities suggest that these species are very closely related. A more thorough comparision between *R. scutata* and R. *newtoni* is not possible until more material of *R. scutata* is collected.

Retrotapes fuegoensis new species
Figure 32, 34–36

Eurhomalea ? cf *fuenzalidai*, Malumián *et al.*, 1978:278, pl.3, fig.4, not *Venus fuenzalidae* Philippi, 1887.

Diagnosis: Shell elongate-oval in outline, anterior margin subtruncated, posterior margin convex. Cardinal teeth lower, narrower than in both *R. striatolamellata* and *R. ninfasiensis*, right anterior tooth straight, vertical, right median tooth shallowly grooved. Lunule very narrow, shallowly concave. Pallial sinus tongue-shaped, much deeper than in *R. striatolamellata*.

Description: Shell large to medium sized, weakly convex, elongate-oval, longer than high. Umbones at 1/9 of dorsal length. Dorsal margin slightly convex, rounding to convex posterior margin; anterior margin subtruncated. Lunule very narrow, shallowly depressed to nearly flat, not inclined toward opposite valve, broader in left valve than in right valve, with slightly marked median radial sulcus, bounded by moderately deep lunular groove. Escutcheon narrow, slightly broader in left valve than in right valve, with strongly sculptured commarginal ridges on both valves. Hinge with anterior tooth vertical, median and posterior teeth inclined backward. Left hinge with strong, high anterior tooth, median cardinal rectangular, bifid, with both parts equal in size, as high as anterior tooth, posterior cardinal lamellar, curved. Right valve with thin anterior tooth, narrow grooved median tooth, thin, deeply grooved posterior tooth. Exterior with strong, rounded, commarginal ridges, more crowded toward ventral margin.

Material examined: Holotype, PU 355–12, left valve, Cerro Castillo height 62.0 mm, length 73.0 mm (Zinsmeister Collection); Paratypes, articulated specimen, DNSG 16.501, height 48.3 mm, length 58.8 mm, right valve DNSG 16.502, height 32.8 mm, length 27.0 mm; six articulated specimens, one left valve, two right (Malumián Collection), and one fragment with left hinge from Estancia La Federica and Cerro Castillo PU 357–16, PU 355–13, DNSG 16.500, 16.503–16.509 (Zinsmeister and Malumián Collections).

Stratigraphic and geographic range: Carmen Silva Formation (late Oligocene-early Miocene), Cerro Castillo and Estancia La Federica, Isla Grande de Tierra del Fuego.

Remarks: *Retrotapes fuegoensis* comes from the uppermost conglomerated beds of the Carmen Silva Formation's exposures at the quarrel of Estancia La Federica and at Cerro Castillo, where it is associated with a highly diverse and well preserved molluscan fauna previously studied by Malumián, Camacho and Gorroño (1978). The outline of *R. fuegoensis* is the most distinctive character that readily distinguishes this species from its congeners. Based on examined material, the Chilean Neogene species *Venus colchaguensis* Philippi, 1887 (=*V. fuenzalidai* Philippi, 1887) may be also included in the genus *Retrotapes*. It differs from *R. fuegoensis* in having an acuminate anterior margin, a poorly defined escutcheon, and commarginal sculpture that consists of widely and uniformly spaced lamellae. *Retrotapes ninfasiensis* may be distinguished from *R. fuegoensis* by its ovate to subrectangular, posteriorly truncated shell, a more concave and broader lunule facing the opposite valve, much larger cardinal teeth, median and anterior teeth that strongly slope backward, and a triangular and shorter pallial sinus than in *R. fuegoensis*. *Retrotapes striatolamellata* differs from *R. fuegoensis* in having a shell that is ovate, more convex, and more acuminate anteriorly, with a lunule that is more concave and broader, and teeth that are larger than in *R.fuegoensis*. *Retrotapes scutata* has a more elongate and ovate shell, with a more concave lunule than *R. fuegoensis*. *Retrotapes antarctica* is characterized by a trigonally suboval shell with umbones placed more posteriorly, an anterior margin that is not truneated, and a smaller triangular pallial sinus than that of *R. fuegoensis*, as well as a right anterior tooth that inclines slightly forward. *Retrotapes newtoni* has an ovate, smaller shell that is not subtruncated anteriorly. It also has a more concave lunule, thinner teeth and a shorter pallial sinus than *R. fuegoensis*. The Recent species *R. exalbida* and *R. lenticularis* have subrectangular and subcircular outlines respectively, deeper, concave lunules and shorter pallial sinuses than *R. fuegoensis*.

DISCUSSION

Fleming (1963) proposed that Neoaustral faunal elements originated in the low latitudes of the Pacific margins during the late Tertiary. However, Zinsmeister (1982,1984) pointed out that at least some components of this fauna would have originated during the early Tertiary in high latitudes of circumpolar regions, and subsequently radiated northward. Antarctic Eocene records of *Aulacomya* Möreh, 1853, *Gaimardia* Gould, 1852, *Gomphina* Mörch, 1853 and *Eurhomalea* Cossmann,1920, led Zinsmeister to consider these to be Neoaustral taxa that originated in the higher austral latitudes much earlier than Fleming suspected.

The transfer to *Retrotapes* of Antarctic species previously assigned to *Eurhomalea* (Zinsmeister, 1984; Stilwell & Zinsmeister, 1992) limits *Eurhomalea* to strata younger than the Pleistocene. *Eurhomalea* most likely originated in Chile during the Pleistocene, later reached the Peruvian littoral fauna, and is now restricted to the eastern Pacific coast. *Retrotapes*, however, is a Neoaustral genus that appeared in Patagonian and Antarctic regions during the early Tertiary.

According to present data, *Retrotapes* first appeared in the southwestern Atlantic Ocean by the Eocene. It occurs in the late Eocene San Julián Formation and the El Chacay Formation of Patagonia, as well as in the Antarctic La Meseta Formation of late Eocene-Oligocene? age. By the early Miocene, *Retrotapes* expanded northward into the middle Chilean region, reached northern Patagonia by the middle Miocene, and attained its northermost distribution (*R. lenticularis* and *R. exalbida*) during the Holocene (Figure 1). Fleming (1963) and Zinsmeister (1982, 1984) agreed that cool seawater temperatures were related to the presence of Neoaustral taxa. Zinsmeister (1982) stated that the development of Neoaustral faunal elements in the early Tertiary of Antarctica reflects the cool water temperatures that existed in that region during the late Eocene. He also considered the absence of Neoaustral genera in earlier Tertiary deposits of South America to indicate the lack of suitable climatic conditions for the development of this fauna.

The present study records a new, Tertiary and Holocene, Neoaustral genus in southern South America, and suggests that it has adapted to a wide range of water temperatures that fluctuated from cool-temperate to warm. Estimates of Antarctic late Eocene paleotemperatures range widely among authors. Kennett (1977) calculated Eocene sea-surface temperatures around Antarctica to have been 9–12°C higher than today, while Feldmann and Zinsmeister (1984) indicated that cool temperate conditions occurred in the area. More recently, Stilwell and Zinsmeister (1992) indicated that, although cool to warm conditions may be inferred from marine invertebrate faunas, the molluscan fossils indicate warm-temperate conditions during the deposition of the La Meseta Formation.

Despite discrepant inferences of paleotemperatures, mollusks reveal that Antarctic conditions during the late Eocene were cooler than those in southern Patagonia during both the Eocene and Oligocene, as well as those recorded during the middle Miocene of northern Patagonia. Del Río (1990, 1994 a,b), inferred warm temperatures for northern Patagonia during the middle Miocene based on the presence of tropical and subtropical genera as *Amusium*, *Flabellipecten*, *Chionopsis*, *Antinioche*, *Hexacorbula*, *Miltha*, *Egeta*, *Arca*, *Dosinia s.str.* and *Lucinisca*. According to del Río (1990, 1994 a,b), middle Miocene temperatures in northern Patagonia would have been similar to those of the tropical Panamic Molluscan Province and the warmest regions of the Gulf and Caribbean Molluscan Provinces. Along the Patagonian littoral, temperatures decreased steadily, with cooler conditions similar to those occurring today having been established by the end of middle Miocene times. Almost 70% of the middle Miocene genera became extinct, including all of the above mentioned tropical and subtropical genera. *Retrotapes*, however, continued to live in this region adapting to the new climatic conditions. Its present distribution is restricted to the warm temperate Argentinian Province and to the cool-temperate Magellanic Province.

Recent advances in our knowledge of Antarctic and Patagonian molluskan assemblages (Zinsmeister & Camacho, 1980; Zinsmeister, 1976,1981,1984; Camacho & Zinmeister, 1986; Griffin, 1991; Stilwell & Zinmeister, 1992) show that the ocurrence of *Retrotapes* in Patagonia and Antarctica, along with several other genera and subgenera, including *Periploma (Aelga)* Slodkewitsch, 1935, *Pteromyrtea* Finlay, 1927, *Lahillia* Cossmann, 1899, *Crassatella* Lamarck, 1799, *Aulacomya* Möreh, 1853, the gastropods *Struthiolarella* Steinmann and Wilekens, 1908 and *Eoscaphella* Stilwell and Zinsmeister, 1992, as well as nuculoids, arcoids (del Río & Camacho, 1997) and veneroids that are presently being studied, reinforces the similarities in paleoclimates of southern South America and the Antarctic continent during the Paleogene, even after the final break-up of the Weddellian Province.

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Iphitus robertsi (Epitoniidae: Nystiellinae), A New Species of Deep-Sea Gastropod from the Gulf of Mexico

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ABSTRACT

Iphitus robertsi, new species, is described on the basis of nine specimens collected in the northern Gulf of Mexico. This new species, which differs from its six congeners in having a bicarinate shell with weakly cancellate sculpture, represents the first record of this genus in the Gulf of Mexico. The co-occurance of this species with deep-sea scleractinian corals suggests that *Iphitus robertsi* may, like its New Zealand congener, may be parasitic on corals.

Key words: Gastropoda, Epitoniidae, new species, Gulf of Mexico, deep-sea.

INTRODUCTION

A recent survey of deep-sea cold seeps of the continental slope of the Gulf of Mexico using the research submersible Johnson-Sea-Link I has led to the discovery of a new species of Epitoniidae from off Louisiana and Texas. The specimens were collected in a vent-free area at a site known as Green Canyon (Roberts *et al.*, 1990), Lease Block 189, during Johnson-Sea-Link I dive 3306. The sea bottom at a depth of 184 m was composed of mixed rocky and biogenic (silty-sandy shell debris) substrate. The description of this new species is based on nine empty shells in different stages of growth that were recovered while sorting three cubic decimeters of biogenic sand under a dissecting microscope. The species diversity of the molluscan fraction of this sample was very high (n=197).

SYSTEMATICS

Family Epitoniidae Berry, 1910
Subfamily Nystiellinae Clench and Turner, 1952
Genus *Iphitus* Jeffreys, 1883
Iphitus robertsi new species
Figures 1–4

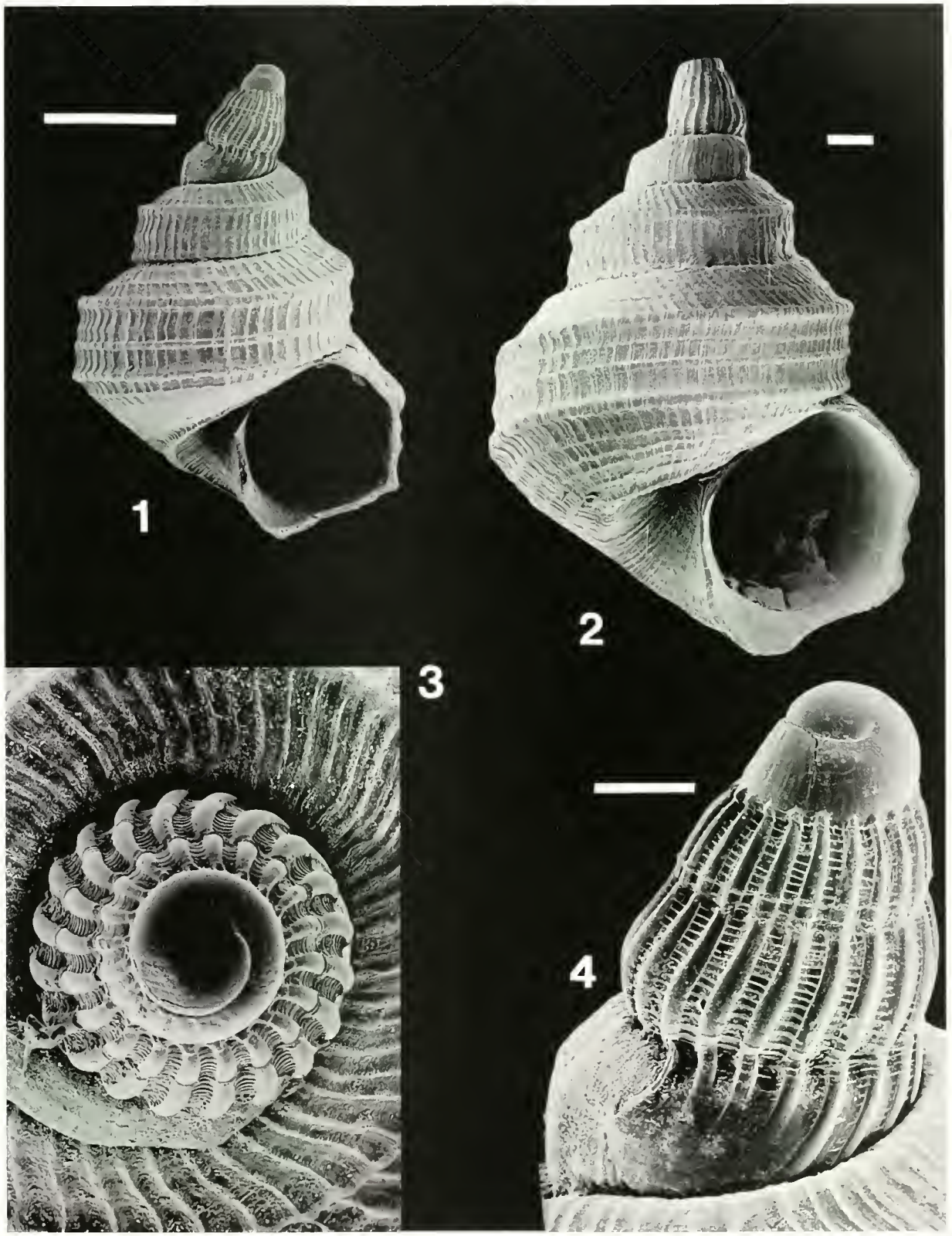
Description: Shell small, relatively fragile, trochiform, holostomatous, umbilicate, with carinate, angular whorls rapidly increasing in diameter. Suture subcanaliculate. Protoconch I of 1¼ smoothly rounded whorls. Protoconch II (larval shell) of 3½ whorls, strongly sculptured by axial ribs and weaker spiral cords. Protoconch brownish, axis inclined by about 10° to teleoconch axis. Teleoconch of 3½ whorls, with strong, spiral sculpture of widely spaced carinae and strong spiral cords. Color whitish, with few, irregular, pale brownish blotches. First half-whorl somewhat rounded, subsequent whorls with two carinae, one in upper third of whorl, the second suprasutural. Strong spiral cords, one between suture and shoulder, one or two between carinae, appear beginning with second whorl. Finer spiral threads visible on body whorl of larger specimens. Shell base with 5–6 spiral threads, innermost bordering deep, wide, infundibuliform umbilicus. Surface of umbilicus sculptured with thin, spiral threads. Axial sculpture of densely spaced threads, producing rectangular, cancellate pattern at intersections with spiral cords, threads, and carinae. Aperture attached to preceding whorl along one face of thin, roughly pentagonal peristome. Only one of nine specimens retained a complete protoconch, the remaining specimens lacked embryonic portion of the protoconch (protoconch I).

Type locality: Green Canyon, Block 189, Gulf of Mexico (27°46.48′N, 93°17.74′W) in 184 m.

Type Material: Holotype, National Museum of Natural History, Smithsonian Institution, Washington, DC, USNM 880185, Paratype USNM 888186; 3 paratypes, Museo di Zoologia, Bologna University, MZB 11621 a,b, MZB 11622; 1 paratype Museum National Histoire Naturelle, Paris; 1 paratype, Houston Museum of Natural Sciences, HMNH 42544, all from the type locality.

Additional Material Examined: 1 shell (Figure 2, accidentally broken), from the type locality.

Etymology: This species is named after Dr. Harry Roberts (Louisiana State University), the Chief Scientist of the research cruise and Scientist-in-Charge of scientific operations during dive JSL-I-3306.



Figures 1–4. *Iphitus robertsi*, new species. Green Canyon, Block 189, Gulf f Mexico (27°46.48'N, 93°17.74'W) in 184 m. **1.** Holotype, USNM 888185, Scale bar = 3 mm **2.** Adult shell, scale bar = 3 mm **3.** Apical and **4.** Lateral views of the protoconch of holotype. Scale bar = 3 mm.

Remarks: Bertolaso and Palazzi (1994) synonymized *Iphitus* Jeffreys, 1883 with *Stylotrochus* G. Seguenza, 1876, which is unavaliable because it is preoccupied by *Stylotrochus* Haeckel, 1862. To date, only six (four extant and two extinct) species of the genus *Iphitus* have been described. The Recent *Iphitus tuberatus* Jeffreys, 1883, *I. cancellatus* Dautzenberg and Fischer, 1896, and *I. marshalli* (Sykes, 1925) inhabit the eastern North Atlantic, while *I. neozelanicus* (Dell, 1956) occurs off New Zealand. The fossil species *Iphitus asperatus* (G.Seguenza, 1886) and *I. papillosocinctus* (G.Seguenza, 1886) are both from upper Pliocene-lower Pleistocene bathyal deposits of Sicily (Palazzi & Villari, 1996). All of these species have been well illustrated (Beu, 1978; Taviani & Sabelli, 1982; Bouchet & Warén, 1986, Bertolaso & Palazzi, 1994, Palazzi & Villari, 1996), and show little similarity to the new species described here. *Iphitus robertsi* superficially resembles *I. marshalli*, which also has strong carinae and spiral cords, but these differ in number and arrangement in the two species. *Iphitus marshalli* also differs in lacking cancellate sculpture. *Iphitus caneellatus*, the only species to be reported from the western Atlantic, differs from *I. robertsi* in having a much coarser reticulate sculpture and a rounded aperture lacking carinae. The fossil legacy of *Iphitus* is quite scant. The oldest record (as *Iphitus sp.*) is from an upper Miocene coral-assemblage in southeastern Spain (Barrier *et al.*, 1991). *Iphitus asperatus* (G. Seguenza, 1886) and *I. papillosocinctus* (G. Seguenza, 1886) are known from Plio-Pleistocene deposits in the Messina region of Sicily (Bertolaso & Palazzi, 1994, Palazzi & Villari, 1996), while *Iphitus tuberatus* occurs in glacial-Pleistocene deposits of southern Italy (Rindone & Vazzana, 1989) and submerged last glacial (Pontinian) tanathocoenoses of the Sicilan Channel (Taviani & Sabelli, 1982).

Habitat: Available ecological data indicates that species of *Iphitus* are parasitic on deep-sea scleractinian corals. Beu (1978) discovered *I. neozelanicus* living embedded in the calices of *Goniocorella dumosa* (Alcock, 1902). While there are no direct observations on any of the Atlantic species, a relationship with deep-sea scleractinian corals has been suggested by Taviani and Sabelli (1982). Bouchet and Warén (1986) noted that *I. tuberatus* occurs with *Lophelia* and that an association is probable. Bertolaso and Palazzi (1994) recorded one shell of *I. asperatus* still associated with a piece of *Lophelia* from the glacial Pleistocene of Calabria (southern Italy). A similar habitat is inferred for *I. robertsi*. As supported by visual observations (H. Roberts, personal communication, September 1992) and sample content, dead and living scleractinian corals (e.g. *Madracis* sp., *Caryophyllia* sp., *Coenosmilia arbuscula* Pourtalès, 1874, and *Balanophyllia* sp.: H. Zibrowius, in litt. 29 October 1993) were abundant at the sampling site. Among the possible hosts, the branching scleractinian *Madracis*, the commonest coral, is the most likely candidate, although no traces attributable to a secondary ectoparasite (Beu, 1978) were visible in our material.

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Verification of the Specific Status of the Endangered Anthony's River Snail, *Athearnia anthonyi*, Using Allozyme Electrophoresis

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ABSTRACT

Although nominally the single surviving representative of a unique pleurocerid taxon, *Athearnia anthonyi* (Budd, in Redfield, 1854) is so rarely collected that even its specific status has been uncertain. We used allozyme electrophoresis to compare a population of *A. anthonyi* to the similar pleurocerid snail, *Leptoxis praerosa* (Say, 1821), co-occurring with it in the Sequatchie River of Tennessee, and to a second population of *L. praerosa* collected approximately 500 km distant. Observed levels of heterozygosity offered no evidence of inbreeding or unusually severe population bottlenecking in any of these populations. Strikingly different allele frequencies at five of the eleven enzyme loci examined, together with differences in shell morphology especially apparent in young individuals, confirmed that *A. anthonyi* and *L. praerosa* are distinct species. Their similarity at the six loci remaining supports previous suggestions that *Athearnia* may be a subgenus of *Leptoxis*.

Key words: *Athearnia*, *Leptoxis*, Pleuroceridae, freshwater gastropods, proteins, enzymes, Tennessee.

INTRODUCTION

The pleurocerid genus *Athearnia* was proposed by Morrison (1971) to include the two species, *Anculosa anthonyi* (Redfield, 1854) and *Anculosa erassa* (Haldeman, 1842), previously but incorrectly included in the genus *Euryeaelon* (Goodrich, 1931). Some authors (Davis, 1974; Burch, 1982) have subsequently considered *Athearnia* to be a subgenus of the widespread genus *Leptoxis*, but we follow Bogan and Parmalee (1983), Garner (1992), and the Federal Register in retaining its generic rank. The distinction between the two nominal *Athearnia* species, *A. anthonyi* and *A. erassa*, has been confused for some years. In any case, since *A. crassa* is generally considered to be extinct (Bogan & Parmalee, 1983), *A. anthonyi* appears to be the sole existing representative of this distinctive pleurocerid taxon.

Historically, populations of *Athearnia* have been recorded from the Tennessee River and its larger tributaries upstream from Muscle Shoals, Alabama, including the Clinch, Powell, Nolichucky, Little Tennessee, French Broad, Sequatchie, and Elk Rivers (Goodrich, 1940). However, the impoundment of the Tennessee drainage that began in the 1930's, improvement of the stream bed for navigation, and general habitat degradation due to farming, mining, and industry eliminated *Athearnia* from the great majority of its former habitat. Bogan and Parmalee (1983) feared that *Athearnia* "may be extinct throughout its range except for a possible relic population."

More recently, it has become clear that small but apparently viable populations of *A. anthonyi* still inhabit lower regions of the Sequatchie River in Marion County, Tennessee, and Limestone Creek in Limestone County, Alabama (Garner, 1992). These snails also survive in at least one channel of the main Tennessee River downstream from the mouth of the Sequatchie (Jenkinson, 1994; Garner, 1994). In early 1994, *A. anthonyi* became the first pleurocerid gastropod formally listed as "endangered" by the United States government (Federal Register 59:17994–17998). In addition to protecting extant populations, the *A. anthonyi* recovery plan (U.S. Fish & Wildlife Service, 1996) calls for the future reestablishment of at least a few populations into portions of the snail's historic range.

Although great interest has focused on the distribution and abundance of *A. anthonyi*, questions remain regarding its taxonomic status. Adult *A. anthonyi* may be confused with large, senescent *Leptoxis praerosa* (Say, 1821), a much more common pleurocerid with which *Athearnia* often occurs. Juveniles of *A. anthonyi* have not often been described. Given that trematode infection may induce extreme and anomalous growth in gastropod hosts (Sturrock, 1966; Hodasi, 1972), it has seemed possible that *Athearnia* may be parasitically castrated, gigantic, *L. praerosa*.

Allozyme electrophoresis has become established as an

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important tool for measuring genetic diversity both within and among populations of pleurocerid snails (Chambers, 1978; 1980; Stiven & Kreiser, 1994). Published work to date has, however, concentrated exclusively on the diverse genus *Goniobasis*, primarily an inhabitant of smaller streams. Genetic variation seems to be unusually low within *Goniobasis* populations, but unusually high between them (Dillon & Davis, 1980). The levels of both intra- and interpopulation gene flow also seem to be unusually low (Dillon, 1988a). Significant gene frequency differences have been reported between samples of *Goniobasis* taken at distances as short as 500 m (Dillon, 1988b). Geographically distant *Goniobasis proxima* (Say, 1825) populations may share no alleles at as many as six enzyme loci of seven studied, yet show no evidence of reproductive isolation (Dillon, 1984; 1986; 1988a). Distinct species of *Goniobasis* generally share alleles at very few enzyme loci (Chambers, 1980; Dillon & Davis, 1980). So although no data have been published on divergences in other pleurocerid genera to this date, there is reason to expect that if *A. anthonyi* is indeed different from *L. praerosa*, differences in allozyme frequencies will be apparent.

In the present work, we use allozyme electrophoresis to compare a population of *A. anthonyi* from the Sequatchie River to a co-occurring population of *L. praerosa* and to a population of *L. praerosa* from the Duck River 500 river kilometers distant (approximately 350 km downstream, then 150 km upstream). In addition to verifying the specific status of *A. anthonyi*, our data also bear on two ancillary questions: the systematic placement of the genus *Athearnia* and the degree to which an important population of *A. anthonyi* may be inbred or bottlenecked.

MATERIALS & METHODS

Athearnia anthonyi and *Leptoxis praerosa* were collected from a site on the Sequatchie River in Marion County, Tennessee. *Leptoxis praerosa* were most common in riffle areas, while *A. anthonyi* were more common on larger submerged objects (rocks, snags, etc.) in the transition areas between riffles and pools. A second sample of *L. praerosa* was collected from the Duck River at Lillard Mill, Marshall County, Tennessee. Voucher specimens of *A. anthonyi* have been deposited in the Ohio State University Museum of Biological Diversity (catalog number 19820). Individuals were transported alive to Charleston, S.C., where the shells were cracked and the digestive glands examined for parasites. Tissues were then frozen in a tris-phosphate buffer at −70°C and examined electrophoretically within one week.

Horizontal starch gel protein electrophoresis was performed on whole animal homogenates as has been previously described (Dillon, 1985; 1992). We initially screened 15 *A. anthonyi* and 14 Sequatchie River *L. praerosa* for variation in 10 enzyme systems: aspartate aminotransferase (AAT), esterases (EST α-napthyl acetate as substrate), glucose phosphate isomerase (GPI), alcohol dehydrogenase (ADH, hexanol as substrate), mannose phosphate isomerase (MPI), octopine dehydrogenase (ODH), phosphogluconate dehydrogenase (6PGD), phosphoglucomutase (PGM), sorbitol dehydrogenase (SDH), and superoxide dismutase (SOD). Simple Mendelian inheritance of codominant alleles has been demonstrated at the 6PGD and PGM loci in *Goniobasis floridensis* (Reeve, 1860) by Chambers (1980) and at the GPI, ODH, and EST1 loci in *G. proxima* by Dillon (1986). It should be noted that a great many esterase allozymes are generally detectable in pleurocerids, but that to date only the strong, slowly-migrating products of the "EST1" locus are genetically interpretable.

An effort was made to examine allozyme phenotypes in as wide a range of buffers as possible. The following gel buffers were employed: Tris-Cit 6.0 (for PGM, GPI, ODH, and MPI), AP 6.0 (for 6PGD), TEB 8.0 (for EST and 6PGD), Poulik (for SDH, ODH, and GPI), and TEB 9.0 (for SOD, ADH, AAT, PGM, and SDH). Recipes for most of these buffers and stains were obtained from Shaw and Prasad (1970) or Harris and Hopkinson (1976), modified for agar overlay in many cases.

Also included in the initial survey for allozyme variation were *G. proxima* standards (population SUGR of Dillon, 1984). *Leptoxis* and *Athearnia* bands were labeled by their mobilities in millimeters relative to this population in a standard buffer. As was the case in 1984, some "hidden" variation was detected at the ODH locus - bands not resolved by the standard Tris-Cit 6.0 buffer were detected with a Poulik buffer. These isozyme classes were labeled "S", "F", and "VF" for their migration in Poulik gels.

After the initial screening, we concentrated our investigations on the five putative enzyme loci apparently varying in our comparison of *A. anthonyi* and *L. praerosa*. Ultimately we examined 37 *A. anthonyi*, 29 *L. praerosa* from the Sequatchie River, and 25 individual *L. praerosa* from the Duck River. Gene frequencies and observed heterozygosities were calculated using BIOSYS version 1.7 (Swofford & Selander, 1981).

RESULTS

Figure 1 compares representative shells from Sequatchie populations of *A. anthonyi* and *L. praerosa*. *Athearnia anthonyi* is distinguishable by the higher shoulder of its whorls, beginning as a pronounced keel (or "carina") but becoming less distinct with age. The oldest *A. anthonyi* are quite smooth, and come to resemble large *L. praerosa*.

Very little evidence of parasitism was detected in either Sequatchie pleurocerid population. Only 2 of 29 *L. praerosa* showed obvious trematode infections, while none of the 37 *A. anthonyi* appeared to be infected. Thus the large sizes attained by individual *A. anthonyi* do not appear to be due to parasitic gigantism.

Figure 1. Growth series for *Athearnia anthonyi* (above—five specimens) and *Leptoxis praerosa* (below) from the Sequatchie River, TN.

No variation was detected between populations of *A. anthonyi* and *L. praerosa* at AAT, ADH, 6PGD, SDH, SOD, or at a faster-migrating PGM locus. Divergence was striking, however, at the five loci listed in Table 1. The two sympatric populations share no alleles at EST1, GPI, MPI, or at the slower PGM locus, "PGMS". And at the ODH locus, *A. anthonyi* appears to be fixed for an allele present at a frequency of only 0.345 in Sequatchie *L. praerosa*.

Although spatially separated by over 500 km, the two *L. praerosa* populations seem to have remained rather similar genetically. Table 1 shows that the differences in allozyme frequency at the GPI, MPI, and ODH loci are significant, but not fixed. The Sequatchie population appears substantially more polymorphic.

Rather low levels of genetic variation were detected within these three populations of pleurocerids, as has been commonly reported in the past. Judging by the 95% criterion, only four of the 15 loci shown in Table 1 could be considered polymorphic. The fit to Hardy-Weinberg expectation at these four loci was very good, however.

DISCUSSION

It is clear that previous misgivings about the specific status of *A. anthonyi* were unfounded. Although not as divergent as typical species of *Goniobasis*, the data presented in Table 1 show clearly that *A. anthonyi* and *L. praerosa* are reproductively isolated in the Sequatchie River. Their shell morphologies are distinct. The greater size attained by *A. anthonyi* appears to be a natural

Table 1. Allele frequencies and observed heterozygosities (H) at variable loci in populations of *Athearnia anthonyi* from the Sequatchie River, *Leptoxis praerosa* from the Sequatchie River, and *L. praerosa* from the Duck River. Sample sizes 37, 29, and 25, respectively.

		Sequatchie R.		Duck R.
Locus	Allele	*A. anthonyi*	*L. praerosa*	*L. praerosa*
EST1	105	0.0	1.00	1.00
	102	1.00	0.0	0.0
	H	0.0	0.0	0.0
GPI	102	0.392	0.0	0.0
	97	0.0	0.586	1.0
	95	0.608	0.0	0.0
	90	0.0	0.414	0.0
	H	0.622	0.552	0.0
MPI	100	0.0	0.034	0.0
	95	0.0	0.966	1.0
	90	1.0	0.0	0.0
	H	0.0	0.069	0.0
ODH	115	0.0	0.086	0.460
	113VF	0.0	0.310	0.0
	113F	1.0	0.345	0.520
	113S	0.0	0.034	0.0
	107	0.0	0.224	0.020
	H	0.0	0.670	0.440
PGMS	103	0.0	1.0	1.0
	90	1.0	0.0	0.0
	H	0.0	0.0	0.0

feature of development, not a consequence of parasitic gigantism.

The level of intrapopulation variation in *A. anthonyi* is low compared to that of most other organisms, but comparable to that seen in *L. praerosa* and in other pleurocerids. We did discover one highly polymorphic locus in *A. anthonyi*, GPI, showing genotype frequencies not significantly different from expectation under Hardy-Weinberg equilibrium (Yates-corrected $\chi^2 = 2.53$). Thus we are unable to detect evidence of inbreeding or an unusually severe population bottleneck.

Previous electrophoretic investigations of *Goniobasis* populations have generally detected higher levels of divergence than we report here between Sequatchie River and Duck River populations of *L. praerosa*. Multiple fixed differences are often observed between *G. proxima* populations isolated in small creeks at distances as great as 500 km. The less dramatic differences between conspecific *Leptoxis* populations reflected in Table 1 may be a consequence of their adaptation to larger rivers. Populations of *Leptoxis* may have inhabited occasional rocky shoals down the length of the Tennessee River before its impoundment, connecting such tributary populations as those of the Sequatchie and Duck Rivers in stepping-stone fashion.

Previous studies have shown greater divergence between pleurocerid species than uncovered here. Dillon and Davis (1980) and Chambers (1980) reported that typical species of *Goniobasis* rarely share any similarity at any allozyme locus. However, *L. praerosa* and *A. anthonyi* were indistinguishable at six of the eleven loci initially screened, and seem to share one fairly common allele at a seventh locus (ODH). This constitutes some support for the nomenclature of Burch (1982) and Dillon (1989) in which *Athearnia* is placed as a subgenus of *Leptoxis*. Regardless of whether they represent a unique genus or a unique subgenus, the populations of *A. anthonyi* now restricted to just a few rivers of central Tennessee are a valuable resource for evolutionary study, and warrant protection at the highest levels.

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Induced Metamorphosis of Freshwater Mussel Glochidia on Nonhost Fish

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ABSTRACT

Intraperitoneal implants of cortisol, an immunosuppressant, suspended in liquid cocoa butter were administered to nonhost fish species. Fish were then infested with glochidia of freshwater mussels to determine if transformation would occur after immune system manipulation. Glochidia of *Venustaconcha sima* (Lea, 1838) (*Villosa iris* complex) transformed on orangethroat darters, *Etheostoma spectabile* (Agassiz, 1854), after injection of cortisol at concentrations ranging from 0.005 to 0.040 mg per g of fish weight. Banded sculpins, *Cottus carolinae* (Gill, 1861), transformed glochidia of *Villosa taeniata* (Conrad, 1834) following cortisol injections ranging from 0.005 to 0.020 mg g. Creek chubs, *Semotilus atromaculatus* (Mitchill, 1818), failed to transform glochidia of either mussel species after cortisol administration. No juvenile mussels were collected from noninjected or sham injected fish during any experiment. Cortisol-induced immunosuppression facilitates metamorphosis of glochidia on some nonhost fish species. Refinement of this technique could provide an alternative means for propagating freshwater mussels, especially for those endangered species that utilize unknown hosts.

Key Words: cortisol, immunosuppression, transformation, glochidia, implants, Unionidae.

INTRODUCTION

The obligate parasitic stage in the life cycle of freshwater mussels on specific host fish may limit reproduction of many populations. Because adequate biological inventories were not conducted before impoundment of most river systems, many fish species were extirpated before identification of glochidial hosts could occur (Schindler, 1989). Hosts are known for only one-quarter of the North American species of mussels (Hoggarth, 1992, Watters, 1994). Although glochidia of a few mussel species have been transformed in a sterile culture medium (Isom & Hudson, 1982), metamorphosis of other species has been less successful. Consequently, artificial propagation of many freshwater mussel species that utilize unknown hosts has not been possible.

Other than the use of known hosts and artificial media, few advancements have occurred in methods of artificial propagation of freshwater mussels. With the relatively recent threat of the zebra mussel, *Dreissena polymorpha* Pallas, 1771, concern for the fate of our native fauna has increased efforts to sustain diversity and protect existing populations, especially endangered or threatened species without identified hosts. Efforts include assessment of relocation into areas with little risk of zebra mussel invasion and the use of mussel refugia such as hatcheries (Shannon *et al.*, 1993).

Host specificity of freshwater mussels is believed to have an immunological basis (Reuling, 1919; Arey, 1932; Meyers *et al.*, 1980). Isom and Hudson (1982; 1984) demonstrated that components in fish blood necessary for initiation of glochidial transformation are not species specific and can be found in the blood of all fish. Moreover, horse and neonatal calf serum are also suitable media for glochidial transformation (Keller & Zam, 1990). The implications of these studies suggest that the immune response of the host is the determining factor in mussel-host specificity.

Immune responses of both host and nonhost fish to glochidia of freshwater mussels have been documented (Reuling, 1919; Arey, 1932; Meyers *et al.*, 1980; Bauer & Vogel, 1987). Responses of host fish consist of host tissue proliferation which encysts the glochidium within a few hours after attachment (d'Eliscu, 1972; Waller & Mitchell, 1989). In host and nonhost species, humoral and cell mediated responses of the immune system occur. These immune responses include the presence of specific antibodies to the parasites (Reuling, 1919; Meyers *et al.*, 1980; Bauer & Vogel, 1987), an increase in eosinophils and other leukocytes around glochidial cysts (Arey, 1932), hyperplastic sloughing of host epithelial tissue (Meyers *et al.*, 1980), and in some cases, cytolitic destruction of the glochidium (Reuling, 1919; Arey, 1932).

Cortisol, a major corticosteroid in teleosts (Idler & Truscott, 1972) is released during stress (Bennett & Wolke, 1987; Schreck, 1990) and produces immunosuppressive

effects. Cortisol can be administered to produce a dose-dependent elevation of plasma cortisol and immunosuppression (Pickering & Duston, 1983). Cortisol reduces lymphocyte concentrations circulating in the blood, reduces lymphocyte participation in inflammation and reduces other inflammatory cells (Pearson *et al.*, 1978). We hypothesized that the effects of cortisol might inhibit the ability of nonhost fish to respond to glochidia by decreasing the number of antibodies and reducing inflammation around glochidial cysts, thus allowing glochidia to attach, encyst, and metamorphose into juveniles. In this paper, we evaluate the effects of cortisol, administered in a vehicle of liquefied cocoa butter, on glochidial metamorphosis.

MATERIALS & METHODS

Collection of fish and mussels: For our experiments, we selected two bradyticite species of mussels based on their narrow host specificity and availability. Gravid *Venustaconcha sima* (Lea, 1838)[1], were collected from the Collins River in Grundy County, Tennessee. Gravid *Villosa taeniata* (Conrad, 1834) were collected from the Roaring River in Overton County, Tennessee. Rockbass, *Ambloplites rupestris* (Rafinesque, 1817), is the only known host of *V. taeniata* (Gordon *et al.*, 1994), and banded sculpin, *Cottus carolinae* (Gill, 1861), is the only known host of *V. sima* (unpublished data). To avoid premature expulsion of glochidia, mussels were kept at approximately 4°C in pans of shallow water until needed. Laboratory established nonhost fish species were used as experimental fish, with the exception of creek chub, *Semotilus atromaculatus* (Mitchill, 1818). The suitability of creek chub as hosts for *V. sima* has not been previously tested in the laboratory; however, examination of wild fish did not reveal any infestations (unpublished data).

A backpack electrofishing unit was used to collect fish from the East Blackburn Fork, Putnam County, Tennessee. Populations of banded sculpins, creek chubs, rockbass, and orangethroat darters, *Etheostoma spectabile* (Agassiz, 1854), are abundant in this stream. No mussels occur in the East Blackburn Fork, and an impassable waterfall downstream prevents any possible upstream movement of fish that may have been exposed to glochidia. Fish were transported back to the laboratory, acclimated to laboratory conditions, and held in 38 liter aquaria.

Implantation and infestation: Pure cocoa butter was melted at a temperature of 40°C. A predetermined amount of cortisol was dissolved in ethanol. Ethanol was used at a rate of 10% the volume of cocoa butter. The dissolved cortisol was suspended in the liquid cocoa butter and allowed to mix in a water bath. Average fish weight was used to calculate the amount of cortisol per gram of fish weight needed to obtain the desired concentration within the fish. Orangethroat darters received 50 µl implants and creek chub and banded sculpins received 100 µl implants.

Infective glochidia were obtained from gravid females and exposed to salt to determine maturity (Zale & Neves, 1982). After fish were anesthetized with tricaine methanesulfonate (MS 222), they were placed on a wet paper towel to reduce the removal of mucus during the injection process. The liquid cocoa butter implant was injected into the peritoneal cavity of the fish with a 1 ml tuberculin hypodermic syringe. The liquid cocoa butter solidified within the cavity of the fish and acted as a solid implant during the experiment. Presumably, cortisol leaked slowly from the implant, but the kinetics of this transfer were not addressed. Pickering and Pottinger (1985) observed maximum mean plasma cortisol levels of 9 and 15 ng/ml for brown trout, *Salmo trutta* (Linnaeus, 1758), that received 10 and 20 mg cortisol respectively. Immediately after cortisol injection, glochidia were pipetted onto the left gills of each fish. Fish were then transferred to fresh water and revived. Each experimental group was kept in a separate aquarium.

Experimental design Treatments varied among experiments, but generally included a known host control group to measure glochidial viability. The no-injection (NI) group verified that the test species did not normally serve as a host. Sham injected fish received injections of pure cocoa butter only, and were used to determine if the injection process or cocoa butter had an effect on glochidial transformation. Cortisol injected fish received concentrations that ranged from 0.005 to 0.040 mg/g. Preliminary experiments determined the feasibility of working with these concentrations, which we initially based on those used by Pickering and Duston (1983) and Pickering and Pottinger (1985).

Aquaria were siphoned daily and the siphonate was examined under a dissecting microscope at 10X to 20X magnification. The number of glochidia and juveniles, water temperature and fish mortality were recorded. Criteria for recognizing juvenile mussels included the presence of two adductor muscle scars, closed valves, and movement within 24 hours of collection. If these criteria were not met, organisms were considered untransformed or partially transformed glochidia. Experiments were terminated when no juveniles were collected from host fish for one week after the last juvenile was collected, or examination of the gills revealed no encysted glochidia. All fish were used for only a single infection experiment.

RESULTS

Metamorphosis of *Venustacoacha sima* on nonhost fish: A total of 58 juvenile *Venustachona sima* were transformed on cortisol injected orangethroat darters. Transformation occurred only on orangethroat darters injected

[1]This species is generally considered a member of the *Villosa iris* complex but was elevated by Gordon (1995). In this paper, we use *Venustaconcha sima* to clearly identify which of the two members of the *Villosa iris* complex occurring sympatarically in the Collins River were used in our experiments.

Table 1. Numbers of juveniles collected from cortisol injected orangethroat darters infested with glochidia of *Venustaconcha sima* in each experiment. Dates indicate when fish were injected and infested. Numbers in parentheses are the average number of juveniles transformed per fish (NI = No-injection).

	Date				
Cortisol (mg/g)	June 6	August 5	March 31	May 17	Total
NI	0	0	0	0	0
0.000	—	0	0	0	0
0.005	17 (1.89)	0	5 (0.36)	3 (0.25)	25
0.010	—	0	4 (0.29)	—	4
0.020	—	—	7 (1.00)	5 (0.50)	12
0.030	—	—	0*	—	0
0.040	—	—	17 (1.70)	0*	17

* Fish mortality was ≥88%.

Table 2. Numbers of juveniles collected from cortisol injected banded sculpins (October and May) and orangethroat darters (December) infested with *Villosa taeniata* in each experiment. Dates indicate when fish were injected and infested. Numbers in parentheses are the average number of juveniles transformed per fish (NI = No-injection).

	Date			
Cortisol (mg/g)	October 27	December 28	May 27	Total
NI	0	0	0	0
0.00	0	0	0	0
0.005	1 (0.13)	—	0	1
0.010	0	0	1 (0.10)	1
0.020	—	0	4 (1.00)	4
0.030	—	0	—	0

in March, May, and June (Table 1). Glochidia from *V. sima* transformed on fish injected with 0.005 to 0.040 mg/g cortisol. Metamorphosis never occurred in sham injected and no-injection (NI) treatment groups during any experiment. Glochidia did not transform on either orangethroat darters or creek chubs injected in August.

Juvenile transformation varied among experiments. For instance, the average number of juveniles transformed per orangethroat darter injected with 0.005 mg/g cortisol ranged from 0.00 to 1.89 among experiments (Table 1). There was a positive correlation between cortisol concentration and metamorphosis within experiments; however, this relationship was confounded by high mortality in some treatment groups. Mortality varied within and among experiments; most deaths occurred soon after injection, and were likely the result of physical injury.

Metamorphosis of *Villosa taeniata* on nonhost fish: A total of six juvenile *Villosa taeniata* were collected from banded sculpins injected with cortisol (Table 2). Transformation of *V. taeniata* glochidia did not occur on orangethroat darters or creek chubs injected with cortisol. In one experiment, nonhost species sloughed glochidia quickly after the infestation. After examination of their gills revealed no remaining glochidia, the fish were reinfested 11 days after the initial infestation. Although creek chubs and banded sculpins retained glochidia longer after the second infestation, metamorphosis did not occur.

Metamorphosis of glochidia on host fish: Transformation of glochidia of *Venustachoncha sima* on the host, banded sculpins, varied between experiments. Banded sculpins transformed 35 juvenile mussels in March and six juvenile mussels transformed on banded sculpins in May. When used as a host control, all banded sculpins were held in one aquarium during each experiment, and individual variation in juvenile transformation could not be assessed.

Because of the aggressive nature of rockbass, the host of *Villosa taeniata*, individuals were kept in separate aquaria. Transformation of glochidia of *V. taeniata* on rockbass varied greatly among individuals and among experiments (Table 3). Juvenile transformation on individual fish ranged from 0 to 13 juveniles in one experiment, to a range of 7 to 262 juveniles in another experiment. There was no clear relationship between the number of glochidia used to infest host fish or water temperature and the number of juveniles recovered from individual rockbass.

DISCUSSION

Cortisol affects leukocyte circulation, influences immune effector mechanisms in lymphocytes, modulates activities of inflammatory mediators, and modifies protein, carbohydrate, and fat metabolism (Tizard, 1988). In fish, this results in immunosuppression and an increased susceptibility to infectious diseases such as furunculosis and bacterial fin-rot (Pickering & Duston, 1983; Pickering & Pottinger, 1985).

The present study has shown that cortisol-induced immunosuppression can facilitate glochidial metamorphosis on nonhost fish species. Presumably, cortisol suppressed the humoral and cell-mediated responses observed in glochidial infestations by Arey (1932) and Meyers *et al.* (1980). Although the strength of fish immune responses after cortisol administration was not measured, transformation occurred on experimental nonhost species only when the immune system was compromised. These results are consistent with the hypothesis that host specificity of freshwater mussels is immunologically controlled.

Glochidia of *Venustachoncha sima* transformed on orangethroat darters in three of four experiments at the lowest concentration (0.005 mg/g) used. Transformation of glochidia of *Villosa taeniata* occurred on banded sculpins during two experiments. For this species, fewer juveniles were collected from fish injected with the same concentration used for orangethroat darters. Creek chubs failed to transform glochidia from either mussel species

Table 3. Total length, number of glochidia recovered, number of juveniles recovered, metamorphosis period, and water temperature (±S.D.) for individual rockbass infested with glochidia of *Villosa taeniata*. Dates indicate when fish were infested.

Date	Total Length (mm)	Temperature (±S.D.)	Number of Glochidia Recovered	Number of Juveniles Recovered	Metamorphosis Period (Days)
Oct. 27, 1993	165	23.75 ± 1.54	986	0	—
	165		798	0	—
	155		693	13	29–31
	169		659	3	29–32
	115		741	1	32
Dec. 28, 1993	51	22.04 ± 1.80	230	7	43–52
	77		124	12	39–52
	63		121	2	34–52
May 27, 1994	160	22.32 ± 1.33	453	249	21–31
	118		421	14	22–28
	98		441	7	23–26
	177		1,221	262	21–39

when injected with cortisol concentrations of 0.005 and 0.010 mg/g cortisol, suggesting that responses to (or uptake of) cortisol varies with species. Threshold levels of cortisol in the blood may exist that allow glochidial transformation, and these levels may not have been reached in creek chubs.

Fish experience periods of natural elevation of plasma cortisol (Idler & Truscott, 1972). Spring and summer elevations of plasma cortisol and other circulating corticosteroids coincide with migration, smoltification of juvenile anadromous salmonids, sexual maturation and spawning of salmonids (Thorpe *et al.*, 1987; Pickering & Pottinger, 1983; Pickering & Christie, 1981; Anderson, 1990). Cortisol concentrations used in this study should have elevated cortisol levels to the physiological range of fish undergoing stress or periods of natural cortisol elevation (Pickering & Duston, 1983; Pickering & Pottinger, 1985; Thorpe *et al.*, 1987). Periods during the life cycle of fish where cortisol elevation has been observed may correspond with the presence of some species of host fish over mussel beds during the discharge of glochidia (Farzaad, 1991). Perhaps mussels evolved to take advantage of weakened immune responses of host species during spawning or other periods of natural immunosuppression.

Host and nonhost fishes exhibit humoral responses of similar strengths, but host and nonhost species reject glochidia at different rates (O'Connell, 1991). Although cortisol injected fish transformed relatively few juveniles during these experiments, transformation per fish was comparable to hosts in some cases. For instance, 0.020 mg/g cortisol injected orangethroat darters transformed an average of 0.50 juvenile *V. sima* per fish in May. Host fish (banded sculpins) only transformed 1.00 juvenile per fish in the same experiment. Individual variations within and among experiments in glochidial transformation of *V. taeniata* on host fish may also reflect a seasonal aspect in the susceptibility of the host (e.g., host spawning season) or the ability of glochidia to be infective at times of the year other than the normal discharge period. We have observed similar variation among trials and individuals in the numbers of juveniles transformed per host for other mussel species. Variation of an order of magnitude or more in the mean number of juveniles transformed per fish has been reported in other studies as well (e.g., Zale & Neves, 1982). Although the number of glochidia attaching to fish is difficult to control and may contribute to some of the variation in the numbers of juveniles transformed, there was no relationship in the apparent numbers (glochidia + juveniles recovered) of *Villosa taeniata* glochidia attaching to individual rock bass and the numbers of juveniles produced.

Additional development of the cortisol-induced immunosuppression of nonhost fish is needed before the technique can be applied on a large scale as a culture method for freshwater mussels. Nonetheless, refinement of this technique could have widespread management implications, especially as a means for propagation of endangered species. This method could also be used to reestablish populations of nonendangered mussel species into new and reclaimed habitat. Application of cortisol immunosuppression techniques to host species could perhaps increase juvenile transformation for reintroduction studies. Also, application of this technique to non-host fish would provide an alternative means of propagating mussel species that have rare or endangered hosts.

The need for further research on the ecological requirements, including identification of fish hosts, habitat, and physicochemical information of mussel species cannot be over emphasized. These ecological requirements hold the answers to developing self-sustaining populations of freshwater mussels. Because survival and fitness of juvenile mussels produced by means of artificial propagation has not been determined (O'Connell, 1991), artificial propagation methods should be used with caution. Any long-term artificial propagation could alter the genetic integrity of mussel species, and possibly prove more harmful than beneficial (Kennedy, 1975; O'Connell,

1991). As a short-term solution to the immediate problem of endangered species, the technique developed in this study offers hope for propagating many species for which hosts have not been identified.

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Gametogenesis of *Mercenaria mercenaria*, *M. campechiensis* and Their Hybrids[1]

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ABSTRACT

Non-native stocks of *Mercenaria mercenaria*, *M. campechiensis* and their reciprocal hybrids were cultured in South Carolina. Histological examination of the gonads revealed a bimodal gametogenic pattern with a major spring spawning peak that continued into summer, followed by a smaller spawning peak in fall. The spring spawning peak of *M. mercenaria* and its maternal hybrid occurred one month earlier than that of *M. campechiensis* and its maternal hybrid. The length of the spring spawning peaks of the hybrids were two months shorter and less intense than those observed for *M. mercenaria* or *M. campechiensis*.

Key words: *M. mercenaria*, *M. campechiensis*, gametogenesis, hybrids, quahogs, reproductive cycle

INTRODUCTION

Loosanoff (1954) was the first to successfully hybridize *Mercenaria mercenaria* (Linnaeus, 1758) and *M. campechiensis* (Gmelin, 1791). Progeny of intra- and interspecific matings were cultured in Virginia (Haven & Andrews, 1957), North Carolina (Chestnut *et al*., 1957) and Florida (Menzel, 1964). In general, *M. campechiensis* grew the fastest, hybrids were intermediate and *M. mercenaria* was slowest, but *M. campechiensis* and its hybrids had lower survival. These early studies confirmed that there were some aquaculture benefits of *M. mercenaria* and *M. campechiensis* hybridization.

The distributions of *M. mercenaria* and *M. campechiensis* overlap along the southeastern United States (Abbott, 1974). Dillon and Manzi (1989) found that hybrids composed as much as 88% of 179 clams collected from Indian River, Florida. Somewhat lower hybridization rate (31%) was observed from a larger sample (n = 1,141) of clams collected from four sites in the Indian River by Bert *et al*. (1993). In Hamlin Creek, South Carolina, pure *M. campechiensis* were present at a frequency of 0.1% in large beds of *M. mercenaria* with negligible hybridization (Dillon, 1992). This suggested that reproductive isolation between the two species may be more pronounced in South Carolina than in Florida.

Dalton and Menzel (1983) documented the gametogenic cycle of young male progeny from laboratory crosses of *M. mercenaria* and *M. campechiensis* cultured in Alligator Harbor, Florida. The bimodal spermatogenic cycle of the female *M. campechiensis* × male *M. mercenaria* progeny was similar to the *M. campechiensis* parental group, whereas, the spermatogenic pattern of the reciprocal hybrid was similar to *M. mercenaria* parents. Hesselman *et al*. (1989) reported a bimodal gametogenic cycle for adult quahogs collected from Indian River, Florida; however, no differentiation of taxa was attempted in that study.

Information on the gametogenic cycle of *Mercenaria* species is limited and there are no studies on adult quahogs of known pedigree. Also, nothing is known of the gametogenic cycle of *M. campechiensis* as far north as South Carolina. The objective of this study was to compare the gametogenic cycle of adult clams of the species *M. mercenaria*, *M. campechiensis*, and reciprocal crosses.

MATERIALS AND METHODS

Mercenaria mercenaria from Milford, Connecticut, and *M. campechiensis* from Port St. Joe, Florida, were spawned in November 1985, January 1986 and February 1986 at Waddell Mariculture Center, South Carolina. Crosses included: *M. mercenaria* female × *M. mercenaria* male (MM); *M. campechiensis* female × *M. campechiensis* male (CC); *M. mercenaria* female x *M. campechiensis* male (MC); and *M. campechiensis* female x *M. mercenaria* male (CM). Individuals from spawns and crosses were held separately in recirculating systems until the quahogs were moved to a nursery at Folly River, South Carolina. Quahogs from the three spawns were combined for each cross on 5 May 1986 and maintained in recirculating systems until planting (10 October 1986). Quahogs of each cross were planted in the Folly River at about 960/m2 in separate protected trays. Av-

[1] Technical Contribution No. 4291 of the South Carolina Experiment Station

erage shell lengths (SL) at planting were 10.3 mm, 17.2 mm, 15.6 mm and 15.0 mm for MM, CC, MC and CM, respectively (Manzi & Hadley, unpubl. data). Samples were collected monthly from September 1987 through November 1987 and January 1988 through October 1988 and preserved in 10% buffered formalin. The quahogs from the CC trays were not sampled in February 1987 and quahogs from MM trays were not sampled in October 1987 and September 1988 because of poor survival. A total of 113, 117, 111 and 78 quahogs were sampled from the CC, CM, MC and MM crosses, respectively.

Gonadal tissue was dissected from the mid-lateral portion of the visceral mass, dehydrated in an alcohol series, cleared in xylene and embedded in paraplast. Sections were cut at 8–10 μm, stained with Harris' hematoxylin and counterstained with eosin.

Slides for each quahog gonad were microscopically examined and gametogenic stages were identified according to the descriptions of Eversole *et al.* (1980), Dalton and Menzel (1983), Ropes (1987) and Hesselman *et al.* (1989). Eight arbitrary stages of male and female gonadal development were used: undifferentiated (follicle wall thicker than in later stages and few, if any, gametogonia near the periphery of the lumen); early developing (small oocytes and primary and secondary spermatogonia with a few spermatocytes found near the follicle wall); developing (larger oocytes adhering to the follicle wall by a peduncle and spermatocytes and spermatids in the lumen); actively developing (all stages of gametogenesis from spermatogonia to spermatozoa and oogonia to mature oocytes present); ripe (lumen filled with large mature oocytes or radiating bands of spermatozoa); spawning (spermatozoa and large mature oocytes still be abundant in the lumen, but gametogenic layer next to the follicle wall noticeably reduced); partially spent (follicle wall contracted and a few mature oocytes and spermatocyte in the lumen); and spent/inactive (few and often phagocytized gametocytes in lumen surrounded by a very thin follicle wall). To facilitate comparison among the parental and hybrid quahogs, a gonadal index was calculated by assigning values to each developmental stage. These values were undifferentiated = 0, early developing = 1, developing = 2, actively developing = 3, ripe = 4, spawning = 3, partially spent = 2, and spent/inactive = 1. Monthly gonadal index values were computed for each pedigree by summing all the developmental stage values for male and female quahogs, and dividing this figure by the number of quahogs in the sample. This procedure has been successfully used by others to study the gametogenic cycle of *M. mercenaria* in New York (Kassner & Malouf, 1982) and in Georgia (Hefferman *et al.*, 1989; Walker & Hefferman, 1994). These monthly gonadal index values were then fitted by spline interpolations to follow the gametogenic cycle over an annual cycle.

RESULTS

Gonadal index curves for progeny from each cross are given in Figure 1. These results indicate a bimodal gametogenic cycle for the progeny of all four crosses; however, the timing of gametogenesis differs among the four progeny. A rapid decline in gonadal index values indicated a spring spawning that continued into summer for *M. campechiensis* (CC) and its maternal hybrid (CM). Average gonadal index values for CC and CM quahogs were 3.62 and 2.28 in April, and 0.50 in August and 0.22 in June, respectively. A second smaller spawning peak was observed in the fall when average gonadal index values for CC and CM decreased from November (3.50 and 1.30) to January/February (2.50 and 0.67).

The pattern of gonadal index values exhibited by *M. mercenaria* (MM) and its maternal hybrid (MC) also indicated a decrease in spring, but roughly one month earlier than CC and CM quahogs. Average gonadal index values for MM and MC decreased from March (2.94 and 3.25) through August (0.64) and June (1.30), respectively. The decrease in gonadal index values observed from September through November also indicated a fall spawning. Although the trend of gametogenesis in the fall for MM and MC was not as clear cut as that of CC and CM, it appears that spawning occurred 1 to 2 months earlier in MM and MC.

The patterns in gonadal index values for the hybrids appear to track that of the maternal parent, but at reduced levels and for shorter periods. For example, the decreases in gonadal index values for spring and fall spawning periods were 3.12 and 1.00 for CC compared to 2.06 and 0.63 for CM quahogs and 2.30 and 1.57 for MM compared to 1.95 and 0.50 for the MC hybrid, respectively. The lengths of spring spawning periods (i.e., time of declining gonadal index values) were approximately 5 months for CC and MM compared to 3 months for CM and MC quahogs.

DISCUSSION

The spring dominant bimodal gametogenic cycle observed in this study has been reported for *Mercenaria* taxa in North Carolina (Porter, 1964), South Carolina (Eversole *et al.*, 1980; Manzi *et al.*, 1985), Georgia (Hefferman *et al.*, 1989; Walker & Hefferman, 1994) and Florida (Dalton & Menzel, 1983; Hesselman *et al.*, 1989). In contrast to Dalton and Menzel's (1983) findings, the timing of the spawning peaks for *M. mercenaria*, *M. campechiensis* and the reciprocal hybrids was not the same; the spring spawning peak of *M. mercenaria* and its maternal hybrid occurred one month earlier than that of *M. campechiensis* and its maternal hybrid. Dalton and Menzel's (1983) failure to detect a difference between the two *Mercenaria* species and each of the species' maternal hybrid may have resulted in part from using small, young, and mostly male quahogs for histological evaluation. *Mercenaria* undergo a juvenile male sexual phase (Loosanoff, 1937) before achieving sexual maturity (Eversole *et al.*, 1980). Sex ratio (1.0 : 1.1, M : F) and average SL (10.5 + 6.4 mm, SD) indicate that the sampled quahogs had completed the juvenile male phase (Eversole *et al.*, 1980; Knaub & Eversole, 1988).

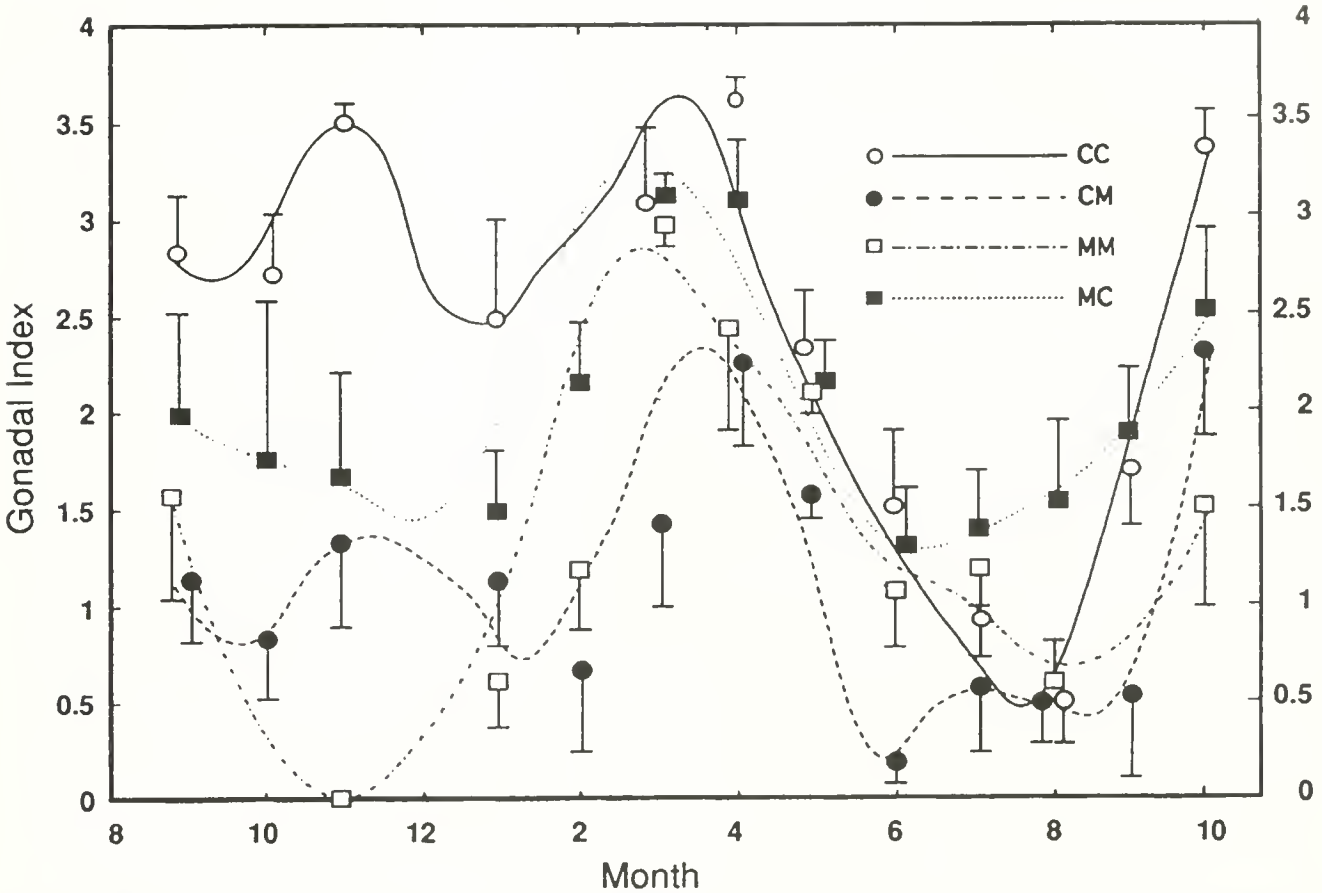

Figure 1. Mean gonadal index with one standard error bar for crosses of *M. mercenaria* female × *M. mercenaria* male (MM), *M. campechiensis* female × *M. campechiensis* male (CC), *M. mercenaria* female × *M. campechiensis* male (MC) and the reciprocal hybrid (CM). Line fitted by spline interpolation.

Hesselman *et al.* (1989) encountered considerable variations in the gametogenic cycle among samples of quahogs collected from Indian River, Florida. Given that both species of *Mercenaria* occur in Indian River, Hesselman *et al.* (1989) speculated one source of the variation could be related to genetic differences in reproductive activity among the taxa. Since then, Bert *et al.* (1993) verified that Indian River contained both *Mercenaria* species and their hybrids. Difficulty associated with defining a gametogenic cycle would be expected if the reproduction cycle is under some genetic control and if closely-related species coexist and hybridization occurs. Currently, there is evidence that different stocks of *M. mercenaria* and *Crassostrea virginica* (Gmelin, 1791) exhibit genetically distinct cycles of gametogenesis and spawning when cultured in a common environment (Knaub & Eversole, 1988; Barber *et al.*, 1991). Barber and his colleagues (1991) suggested that oyster stocks had genetically different environmental requirements necessary for initiating gametogenesis and eventually for cuing spawning.

Dillon and Manzi (1989) suggested that spawning time and habitat separation could be possible mechanisms maintaining the genetic integrity of the two *Mercenaria* species. In the Indian River, Florida, where *Mercenaria* coexist, 88% and 31% of 179 and 1,141 collected quahogs were naturally occurring hybrids, respectively (Dillon & Manzi, 1989; Bert *et al.*, 1993). Farther north in Hamlin Creek, South Carolina, only about 0.1% of thousands of quahogs examined were *M. campechiensis*, and hybrids were rarer still (Dillon, 1992). Although the timing of the gametogenic cycles of introduced stocks of *M. mercenaria* and *M. campechiensis* differ in the spring, sufficient overlap may exist for hybridization of native *Mercenaria* in South Carolina. The fact that *Mercenaria* hybrids were encountered less frequently in South Carolina than in Florida indicates that spatial separation or some other fact may be more important for reproductive isolation than the temporal differences in spawning. It is interesting that the *M. campechiensis* and hybrids identified by Dillon (1992) were collected from a rather unique South Carolina habitat, one characterized by ocean-derived high-saline water, firm substrate covered by deep water and a community of stenohaline biota (e.g., *Chione cancellata* Linnaeus, 1767). A survey of *M. mercenaria* habitat in South Carolina revealed that most of the areas with clams were mud and sand covered by shallow mixohaline waters (Anderson *et al.*, 1978). It

is anticipated that *Mercenaria* hybridization will become a rarer event in higher latitudes of the Atlantic coast as contiguous habitats meeting the species-specific requirements of both species become less available.

Early studies indicated a growth advantage of *M. mercenaria* and *M. campechiensis* hybridization (Haven & Andrews, 1957; Chestnut *et al.*, 1957; Menzel, 1964) possibly because the hybrids have a shorter and less intense spawning period than the two species. However, Eversole and Hefferman (1995) also observed that gonadal neoplasia occurred more frequently and in a more advanced stage in the hybrids than in *M. mercenaria* and *M. campechiensis*. Aquaculturists need to be aware of both the favorable and unfavorable attributes associated with hybridization programs when trying to improve quahog performance.

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The Modern Terrestrial Gastropod (Land Snail) Fauna of Western Wisconsin's Hill Prairies

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ABSTRACT

This paper describes the first survey and quantified analysis of the terrestrial gastropod fauna associated with xeric "hill prairie" and related dry habitats in western Wisconsin's Driftless Area. A region of 35,000 km² in the Midwestern U.S.A., the Driftless Area was surrounded on three sides, but never covered by late Pleistocene glacial ice. In all, 44 separate vegetation detritus samples, each with a volume of 0.5 to 2.0 liters, were collected in nine western Wisconsin counties. These samples contained 10,900 gastropods, with 29 taxa represented. The sampled hill prairies were found to have localized, high-density gastropod populations characterized by a small number of abundant taxa. One species, *Gastrocopta procera* (Gould, 1840) is currently listed as Threatened in Wisconsin. This species occurs at disjunct prairie habitats along the dissected valley of the Mississippi River that may represent a relict distribution for this species.

Key words: Land snails, biogeography, Midwestern U.S.A.

INTRODUCTION

This report describes the results of a baseline survey to assess the living terrestrial gastropod fauna associated with the xeric "hill" prairies (Curtis, 1959:275–276) of Wisconsin's Driftless Area. The study provides the first systematic assessment of gastropod abundance and species diversity at hill prairie and associated dry locations in nine western Wisconsin counties. From the standpoint of terrestrial gastropod distribution, this area is one of the least known regions in eastern North America (Hubricht, 1985:2), although some research has been undertaken in the past (J. P. E. Morrison, 1929; Levi & Levi, 1950).

The physical setting of western Wisconsin is varied and complex. The heavily dissected hill country of this region has been assigned to the Western Upland physiographic province by Martin (1965:42–43). Southwestern Wisconsin is within the Driftless Area (Martin, 1965: 82–83), located primarily within the Western Upland, with smaller portions extending into the adjacent states of Iowa, Illinois, and Minnesota. The Driftless Area, as its name implies, lacks evidence of glaciation during the later Pleistocene (Mickelson *et al.*1982:155–169), and covers an area of 35,000 km², about 75% of which is in southwestern Wisconsin (Roosa, 1984:43). The Driftless Area's topography is characterized by steep-sided, stony valleys dissecting the uplands with dendritic patterns of small stream development. The narrow upland ridges and escarpments of the larger valleys exhibit up to 150 m of relief. The two prominent rivers crossing the region are the Mississippi, which forms the western boundary of Wisconsin, and the Wisconsin River, which drains much of central and southwestern Wisconsin.

Western Wisconsin is situated between the tall-grass prairies to the west and the deciduous forest to the east. The southwestern portion of the state has been assigned to the "prairie-forest province" lying to the south of the floristic tension zone of Curtis (1959:15) and is characterized by its mosaic of vegetation communities. The structure and position of these communities have resulted from a variety of factors, including topography, climate, periodic burning of prairies, and underlying soils and bedrock. At the time of Euro-American settlement, four distinct vegetation communities were predominant: prairie, oak savanna, southern oak forest, and southern mesic forest. The most extensive prairie community was the mesic prairie type, dominated by grasses such as big bluestem (*Andropogon gerardi*), Indian grass (*Sorghastrum nutans*), and forbs. Prairies by definition support fewer than one tree per 0.4 ha. In western Wisconsin, mesic prairies formed large tracts on gently rolling uplands, particularly south of the Wisconsin River in Iowa, Grant, and Lafayette counties. Nineteenth-century travelers who journeyed from forested regions in eastern North America often described the extensive tall-grass prairies they first encountered in western Wisconsin. One of the best-known mesic prairies was the Military Ridge Prairie, which ran from the town of Verona in Dane County, to the northwestern corner of Grant County (Curtis, 1959:262–264).

Xeric prairie communities in the Driftless Area were locally conspicuous but spatially circumscribed (figures 1, 2). These xeric hill or "goat" prairies occupied steep south- or southwest-facing slopes and made up only a

Figure 1. Brady's Bluff hill prairie in Trempealeau County, Wisconsin. Arrow points to the sampling location (UWA-3026) shown in figure 2. View is toward the north, with the Mississippi River in the foreground.

small fraction of the Driftless Area's vegetational landscape. Hill prairies developed on the thin soils overlying dolomite outcrops with excessive runoff. These locales have a uniformly high calcium content and a pH of 8.0 or more (Curtis, 1959:275–276). The four most common plant species on these hill prairies, in order of abundance, are little bluestem (*Andropogon scoparius*), sideoats gama grass (*Bouteloua curtipendula*), big bluestem, and silky aster (*Aster sericeus*). Overall, Asteraceae make up 27.5%, Poaceae 13.7%, Fabaceae 5.3%, Rosaceae 4.6%, and Asclepiadaceae 4.6% of the hill prairie community (Curtis, 1959:269).

The upland mesic prairie communities in western Wisconsin originated during the mid-Holocene warm/dry Atlantic climatic episode (Bartlein & Webb, 1982: 80; Maher, 1982:132). In later Holocene times, most of the region's prairie stands were maintained by frequent burning, which is well documented by both historic accounts (Anderson, 1954:15–22; Martin, 1965) and the presence of charcoal in regional pollen profiles (Davis, 1977:204–213). Soils that formed under mesic prairie communities, particularly Tama and Dodgeville silt loams (Hole, 1976:140–173, Plate 7) are widely distributed along the upland ridges of western Wisconsin. The mesic prairies are gone from western Wisconsin today, replaced by agricultural fields.

MATERIALS AND METHODS

In 1979 the author collected two vegetation detritus samples from a hill prairie in Crawford County, Wisconsin. These samples contained 16 gastropod taxa, including one species not previously recorded in Wisconsin, *Gastrocopta procera* (Gould, 1840). *Gastrocopta procera* is a species associated with prairie/savanna vegetation communities in regions with a frost-free season of 160 days or more (Reigle, 1963; Baerreis, 1980:108–109). In 1985 two additional hill prairie vegetation detritus samples were collected in La Crosse County, Wisconsin. One of these samples also contained *G. procera*. Personnel at the Wisconsin Chapter of The Nature Conservancy (TNC) and the Wisconsin Department of Natural Resources (WDNR) showed interest in developing an inventory of hill prairie gastropod communities, leading the author to collect and analyze 40 additional samples from western Wisconsin hill prairies and related habitats during 1986 and 1987.

Hill prairies sampled for gastropods included a variety

Figure 2. Brady's Bluff hill prairie in Trempealeau County, Wisconsin. Sampling location UWA-3026 is at the upslope side of the detached boulder. Photo looks west, with the Mississippi River on the left.

of TNC, WDNR, and privately owned xeric settings in nine western Wisconsin counties, eight of which border the Mississippi River: from south to north, they are Grant, Lafayette, Crawford, Vernon, La Crosse, Trempealeau, Buffalo, Pepin, and Pierce (table 1). Whenever possible, TNC and WDNR properties were emphasized, under written agreement with those agencies. In all, 35 samples were taken and analyzed at 19 separate hill prairie settings (figure 3).

Specific sampling locations were selected by searching each hill prairie to identify areas with living gastropods or fresh shells. The most productive locations occurred where relatively dense stands or clumps of prairie grasses abutted isolated bedrock exposures, forming "pockets" that would hold accumulations of vegetation detritus. Although some of the sampled hill prairies (e.g., Rush Creek South in Vernon County) cover several acres, the gastropods were primarily limited to discrete concentrations within the larger areas. These localized gastropod populations, often restricted to less than a square meter, seem to represent small, isolated communities within the hill prairie setting. Given this distribution pattern, random sampling would have resulted in the recovery of fewer species and fewer individual snails.

In addition to the hill prairie settings, nine samples were taken in four counties (Grant, Lafayette, Crawford, and Vernon) from what were considered to be "high-stress" habitats for gastropods (table 2). The habitats that are referred to as high-stress appeared to represent the driest locations that could be expected to support living gastropod communities. These locations generally lacked xeric prairie vegetation and consisted of a thin layer (<2 cm) of organic detritus on dolomite bedrock exposures. They were often adjacent to some canopy cover from woody vegetation (birch, cedar, or oak), but were otherwise exposed to the extremes of Wisconsin's climate.

One to four samples, each with a volume of 0.5 to 2.0 liters, were taken at each hill prairie or high-stress habitat. Each sample consisted of vegetation detritus and approximately 1.0 cm of underlying soil taken among prairie plants adjacent to or against rock exposures. Sampled locations were marked on USGS topographic maps and usually photographed. Each sample was measured by volume in the laboratory and then water-screened, with the gastropods and other material retained in geologic sieves (Tyler #40, mesh size 0.425 mm). The screen-captured residue was then dried and systematically searched for gastropods under a low-power (10×) binocular microscope. All gastropod shells and potentially identifiable shell fragments were removed from the

Table 1. Locations of western Wisconsin hill prairie gastropod samples

County	Location	UWA	Date	Legal location	Aspect	Slope	Vegetational setting
Grant	Dewey Hts	3051	4/87	T3N R5W Sec. 13; NE, NE, SW	W	[1]S	Grasses, sumac, cedar adj. to dolomite outcrop
	Zimmer	3014	6/86	T4N R6W Sec. 11; NE, NE	W	S	Grasses, red cedar
Lafayette	M Mound	3040	3/87	T3N R1E Sec. 5; SW, SW	S-SW	S	Grasses, sumac adj. to dolomite outcrop
Crawford	Gran Grae	2547	6/79	T7N R5W Sec. 19; SW, NE, NE	S-SW	S	Grasses, forbs adj. to dolomite bedrock
		2576	6/79	T7N R5W Sec. 19; SW, NE, NE	S-SW	S	Grasses, forbs adj . to dolomite bedrock
	Leitner Hollow	3055	8/87	T9N R6W Sec. 33; W, NE, NE	S-SW	[2]M	Grasses, forbs adj. to dolomite bedrock
		3056	8/87	T9N R6W Sec. 33; W, NE, NE	S	M	Grasses, forbs adj. to dolomite bedrock
	Rush Creek	3035	5/86	T10N R6W Sec. 6; SE, SW	W	S	Grasses, forbs adj. to dolomite bedrock
		3036	5/86	T10N R6W Sec. 6; SE, SW	S	S-M	Grasses, forbs
		3058	11/85	T10N R6W Sec. 6; NW, SW	S	M	Grasses, forbs adj. to dolomite bedrock
Vernon	Battle Bluff	3043	2/87	T11N R7W Sec. 4; W, SW, NE	SW	S-M	Grasses, forbs, red cedar stump w/dolomite outcrop
		3053	2/87	T11N R7W Sec. 4; W, SW, NE	SW	S	Grasses at dolomite outcrop
	Victory	2962	9/85	T12N R7W Sec. 28; SW, NE, NE	SW	S	Grasses on dolomite bedrock
		2963	9/85	T12N R7W Sec. 28; SW, NE, NE	SW	S	Grasses
		3037	4/86	T12N R7W Sec.28; SW, NE, NE	SW	S	Grasses
La Crosse	Experimental	2987	4/86	T16N R5W Sec. 30; SE, NE	S	S	Grasses w/sumac
	Farm	3005	3/85	T16N R5W Sec.30; S, NE, NE	SW	S	Grasses
		3006	3/86	T16N R5W Sec. 30; S, NE, NE	SW	M	Grasses in sumac/birch at dolomite outcrop
	Hixon Forest	3029	3/86	T16N R7W Sec. 34; E, SE, NW	S-SW	M	Grasses at dolomite outcrop
		3030	3/86	T16N R7W Sec. 34, E, SE, NW	SW	M	Grasses in sumac/birch at dolomite outcrop
		3042	4/87	T16N R7W Sec. 34, E, SE, NW	SW	M	Grasses at dolomite outcrop; adj. birch tree
		3057	3/87	T16N R7W Sec. 34, E, SW, NW	SW	M	Grasses
	Bird Bluff	2964	9/84	T17N R7W Sec. 28, NW, NW, SE	SW	S	Grasses at dolomite outcrop
Trempealeau	Brady's Bluff	3026	6/86	T18N R9W Sec. 20; N, NE, SW	S-SW	M	Grasses adj. to dolomite outcrop
Buffalo	Landfill Rd	3024	5/86	T21N R12W Sec. 9; SE, NE, SW	W	S-M	Grasses, forbs w/sumac adj. to dolomite boulder
		3025	5/86	T21N R12W Sec. 9; SE, NE, SW	W-SW	S	Grasses, forbs w/sumac over dolomite bedrock
Pepin	Stockholm	3023	5/86	T24N R16W Sec. 35; NW, SE, SW	S	S	Grasses adj. to cedar on dolomite bedrock
	5-Mile Prairie	3031	11/86	T23N R14W Sec. 15; SW, NE, SW	S	S-M	Grasses w/sumac adj. to dolomite outcrop
		3041	11/86	T23N R14W Sec. 15; SW, NE, SW	S	M	Grasses w/sumac adj. to dolomite outcrop
	Lake Pepin	3048	4/86	T23N R15W Sec. 8; SE, NW, NE	S-SW	M	Grasses, forbs w/sumac adj. to dolomite outcrop
		3049	4/86	T23N R15W Sec. 8; SE, NW, NE	SW	M	Grasses
Pierce	Maiden Rock	3047	4/87	T24N R13W Sec. 23; NW, NW, SW	S-SW	S	Grasses, forbs w/sumac adj. to dolomite outcrop
	Rush River	3046	4/87	T24N R13W Sec. 9, NE, SW, SW	SW	M	Grasses, forbs w/sumac adj. to dolomite outcrop
	Hager City	3044	4/87	T25N R18W Sec. 35; NW, SE	S-SW	M	Grasses, forbs adj. to dolomite bedrock
		3045	4/87	T25N R18W Sec. 35; NW, SE	W	M	Grasses w/sumac adj. to dolomite bedrock

[1] S = slight slope, 0–15°
[2] M = moderate slope, 15–30°
Grasses are primarily little and big bluestem and side-oats gama grass
UWA = University of Wisconsin Laboratory accession number
Aspect = direction slope was facing.

Table 2. Western Wisconsin high-stress gastropod samples locations.

County	Location	UWA	Date	Legal location	Aspect	Slope	Vegetational setting
Grant	Dewey Hts.	3050	4/87	T3N R5W Sec. 13: NE, NE, SW	W	[1]S	Grasses in cedar root shade of cedar on dolomite ledge
		3052	4/87	T3N R5W Sec. 13: NE, NE, SW	W	S	Grasses shaded by oaks, humus on detached boulder
Lafayette	M-Mound	3038	7/78	T3N R1E Sec. 5; SW, SW	S	S	Grasses on thin soil on detached dolomite bedrock
Crawford	Rush Creek	3032	4/86	T99N R7W Sec. 1; NW, SW, NW	SW	S	Grasses on thin soil on detached dolomite bedrock
		3033	4/86	T99N R7W Sec. 1; NW, SW, NW	W	S	Cavity in detached boulder w/humic soil, some grass
		3034	4/86	T99N R7W Sec. 1; NW, SW, NW	W	S	Top of flat-topped boulder (3033), thin soil
Vernon	Cedar Valley	3027	9/86	T14N R6W Sec. 21: SE, NE, NE	S	S	Grasses on dolomite rock, humic soil
		3028	9/86	T14N R6W Sec. 21: SE, NE, NE	S	[2]M	Leaf mold, cedar on sandstone
		3039	9/86	T14N R6W Sec. 21: SE, NE, NE	S	M	Leaf mold, cedar on sandstone

[1] S = slight slope, 0–15°.
[2] M = moderate slope, 15–30°.
[3] Grasses are primarily little and big bluestem and side-oats gama grass

Table 3. Gastropod assemblages from western Wisconsin hill prairies.

County:		Grant		Lafayette	Crawford							Vernon				
Sample location:		Dewey Hts.	Zimmer	M-Mound	Gran	Grae	Leitner Hollow		Rush Creek			Battle Bluff		Victory		
UWA:		3051	3014	3040	2547	2576	3055	3056	3035	3036	3058	3043	3053	2962	2963	3037
Taxon:	Sample volume (L):	1.1	0.75	1	NR	NR	0.8	0.7	0.8	0.8	1	2	1.8	1	1	0.75
Stenotrema barbatum	(C.H. Clapp, 1904)	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mesodon clausus	(Say, 1821)	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Euconulus fulvus	(Muller, 1774)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Glyphyalinia indentata	(Say, 1823)	2	2	6	—	3	—	—	7	14	—	60	7	1	—	2
Nesovitrea electrina	(Gould, 1841)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hawaiia minuscula	(Binney, 1840)	—	7	—	2	4	2	14	1	11	7	12	3	6	9	3
Zonitoides arboreus	(Say, 1816)	—	—	—	—	13	—	2	2	8	—	3	—	—	1	1
Striatura milium	(E.S. Morse, 1859)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Striatura sp.		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Deroceras laeve	(Muller, 1774)	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Anguispira alternata	(Say, 1816)	—	—	18	—	—	—	—	—	—	—	—	—	—	—	—
Heliodiscus parallelus	(Say, 1817)	9	—	—	4	35	1	29	—	16	8	79	26	—	3	20
Helicodiscus singleyanus	(Pilsbry, 1890)	2	—	—	1	—	—	5	—	23	4	4	36	3	—	12
Punctum minutissimum	(I. Lea, 1841)	4	6	—	—	2	—	—	—	6	1	8	1	10	4	5
Succineidae		3	—	2	—	1	—	2	1	1	—	—	—	—	—	—
Strobilops labyrinthica	(Say, 1817)	9	6	—	9	14	4	2	13	45	28	—	—	3	3	2
Strobilops affinis	Pilsbry, 1893	6	8	—	—	—	—	—	—	—	—	—	—	—	—	—
Strobilops sp.		—	17	—	—	—	—	3	1	42	5	—	—	2	1	—
Gastrocopta armifera	(Say, 1821)	11	32	18	39	27	12	98	2	3	59	34	11	4	—	2
Gastrocopta contracta	(Say, 1822)	5	2	6	1	—	—	5	2	16	—	—	1	2	1	1
Gastrocopta holzingeri	(Sterki, 1889)	39	9	5	101	14	—	2	13	27	34	30	33	69	37	53
Gastrocopta pentodon	(Say, 1821)	7	8	—	7	29	—	—	—	9	13	23	12	16	21	3
Gastrocopta corticaria	(Say, 1816)	3	—	1	2	1	—	3	—	1	—	—	1	—	—	—
Gastrocopta procera	(Gould, 1840)	10	13	—	2	5	14	4	3	7	1	21	12	8	—	10
Pupoides albilabris	(C.B. Adams, 1841)	4	10	2	—	—	13	22	—	6	4	51	9	—	—	—
Columella edentula	(Draparnaud, 1805)	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Vallonia pulchella	(Muller, 1774)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Vallonia costata	(Muller, 1774)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Vallonia parvula	Sterki, 1893	—	—	—	75	14	2	29	2	5	27	51	33	1	6	10
Vallonia perspectiva	Sterki, 1892	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—
Vallonia sp.		20	—	7	108	15	7	53	1	6	54	68	64	5	3	13
Cochlicopa lubrica	(Muller, 1774)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Juveniles		30	15	4	NR	NR	20	28	5	24	35	58	33	56	46	61

NR = Not recorded.

detritus and held for identification. Specimens were later identified, cataloged, and stored in glass vials with identification/provenance labels. The nomenclature used in this paper follows Turgeon *et al.* (1988). Voucher specimens of each taxon collected were deposited in the Field Museum of Natural History.

RESULTS

The 41 samples taken during this survey contained 10,900 gastropods or gastropod shells representing 29 species. Of these, the 35 hill prairie samples contributed 8,664 gastropods with all 29 taxa represented (table 3). The three most common and widespread species found at the hill prairie sites were *Gastrocopta armifera* (Say, 1821), *Gastrocopta holzingeri* (Sterki, 1889), and *Gastrocopta pentodon* (Say, 1821). Each of these species contributed more than 11% of the total number of snails and was present in 30 or more of the 35 samples; two of the three were represented in all nine counties sampled (table 4). Each of the next 12 most abundant taxa represented 1.3% to 8.7% of the total number of snails, occurred in 14 to 28 of the 35 samples, and was found in at least six of the counties surveyed. Together, these 15 most abundant taxa made up over 96% of the hill prairie gastropods. The majority of the snails represented are taxa that typically occur in prairie or savanna habitats. The remaining 14 species made up less than 4% of the gastropods, and most occurred in relatively few samples.

The nine samples taken from high-stress habitats contained 2,236 gastropods of 20 taxa (table 5). All of these

Table 3. Extended.

La Crosse									Trempealeau	Buffalo		Pepin					Pierce			
Experimental Farm			Hixton Forest				Bird Bluff	Brady's Bluff	Landfill Rd.		Stockholm	Five-Mile Prairie		Lk. Pepin		Maiden Rock	Rush Riv.	Hager City	
2987	3005	3006	3029	3030	3042	3057	2964	3026	3024	3025	3023	3031	3041	3048	3049	3047	3046	3044	3045
1	1.5	1	1	1.2	1.1	0.8	0.8	1	1	1	1.5	1.1	1	1.5	0.65	1	1.7	1.1	0.6
—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	2	—	4	—	—	1	4	1	—	1	—	—	1	—	—	—	—
—	5	2	11	22	3	1	4	5	12	—	3	5	15	11	11	3	20	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
—	—	1	27	1	3	—	—	1	—	2	5	—	4	89	36	27	42	6	43
1	3	1	5	2	1	—	—	2	20	1	—	—	—	5	3	1	—	—	2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4
—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	1	—	—	—	26	4	—	—	5	2	—	—
—	8	12	61	5	6	—	—	19	41	5	4	41	9	40	4	10	5	1	1
—	—	2	—	—	—	—	—	—	—	—	2	1	—	5	—	—	15	—	—
9	—	2	22	20	23	23	—	12	36	—	—	31	20	13	24	23	14	4	—
—	—	—	36	1	14	1	—	3	4	—	1	—	—	—	2	3	—	1	2
1	—	1	2	2	—	—	—	—	1	1	4	10	23	24	14	5	2	—	12
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6	—	—	15	4	—	—	—	—	5	—	1	59	31	55	101	—	1	3	13
—	—	29	58	4	141	11	5	15	11	16	42	1	4	13	7	13	80	56	97
1	—	1	3	3	7	3	—	—	18	—	1	17	33	6	7	4	16	1	1
34	2	63	—	24	3	11	33	5	—	10	31	—	—	19	45	23	53	27	4
23	5	13	79	25	9	12	1	11	48	—	13	51	23	76	53	11	41	22	22
—	—	—	—	—	7	—	—	—	—	2	—	—	—	—	—	8	—	—	—
1	—	10	14	—	1	5	—	14	—	1	—	—	—	—	—	—	—	6	3
—	—	22	28	—	9	—	1	6	2	12	13	3	—	9	12	3	45	15	10
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	6	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	41	—	33	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	1	71	3	—	19	32	—	—	9	19	8	60	12	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	4
—	—	—	—	—	54	—	480	6	—	42	43	—	—	10	19	—	54	41	21
—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—	—	—
41	4	53	83	10	102	44	78	15	53	21	48	31	16	31	77	21	79	45	44

taxa were also represented at hill prairie sites; however, the rank order of the species was different in the high-stress samples. The first- and second-ranked species at hill prairies, *Gastrocopta armifera* and *Gastrocopta holzingeri*, ranked second and fifth in the high-stress samples and contributed 38.5% of all snails (table 6). Three other species, *Gastrocopta corticaria* (Say, 1816), *Vallonia perspectiva* Sterki, 1892, and *Vallonia costata* (Müller, 1774) contributed 52.5% of the gastropods in the high-stress samples, ranking first, third, and fourth respectively, while ranking sixteenth, nineteenth, and twenty-first in the hill prairie samples. Together, these five most abundant forms represented 91.1% of the species recovered in the high-stress habitats. The difference in species composition between the assemblages probably reflects the differences between the sampled habitats.

DISCUSSION

The hill prairies of western Wisconsin host a fairly diverse community of terrestrial gastropods, with some 15 species being relatively abundant and widespread. A comparison of these survey results with Hubricht's (1985) county listings for eastern North America revealed that the hill prairie survey contributed 130 new county records, and eight species that had not been recorded previously in Wisconsin (table 4).

One taxon worthy of special comment, *Gastrocopta procera*, is currently listed in Wisconsin as a state Threatened species. *Gastrocopta procera* finds its preferred habitat in prairie and savanna settings. This species does not live in the closed-canopy moist woodlands of western Wisconsin (Theler, 1992). The northernmost

Figure 3. Sampling location in western Wisconsin. (*Base map used with permission of the Wisconsin Geological and Natural History Survey.*)

modern range of *Gastrocopta procera* in North America is represented by the small populations found at hill prairie locations in western Wisconsin described in this paper. These hill prairies are remnants of more extensive upland prairies and savannas that covered ridgetops and well-drained south- and west-facing exposures in much of southern and western Wisconsin at the time of Euro-American settlement (Anderson, 1954; Curtis, 1959: 262–264). These prairies became established during the mid-Holocene warm/dry Atlantic climatic episode, about 8,000 to 5,000 years ago (Wendland, 1978:278; Wendland & Bryson, 1974). The Atlantic episode witnessed the eastward expansion of the wedge of prairie and savanna often called the Prairie Peninsula (Wright, 1968). The climatic episodes that followed the Atlantic were cooler and/or moister, and the prairie/savanna vegetation communities were reduced (Wendland, 1978) to stands that were either fire maintained or situated on topographically controlled droughty exposures, such as hill prairies. The cessation of prairie fires with the onset of Euro-American settlement during the nineteenth century led to the loss of most fire-maintained prairies in Wisconsin (Curtis, 1959:295–305). The Mississippi River valley has an ameliorating climatic effect, extending the

Table 4. Rank order and assemblage frequency of summed terrestrial gastropods from 35 western Wisconsin hill prairie samples.

Taxon	Rank	Number of assemblages in which taxon occurred	Number of specimens	%	Number of counties recorded	Number of new county records	New state records
Gastrocopta armifera	1	32	955	16.5	9	8	
Gastrocopta holzingeri	2	30	862	14.9	9	9	
Gastrocopta pentodon	3	30	686	11.8	8	7	
Helicodiscus parallelus	4	28	502	8.7	8	7	
Hawaiia minuscula	5	27	368	6.4	8	8	
Gastrocopta contracta	6	27	164	2.8	8	7	
Strobilops labyrinthica	7	26	240	4.1	7	5	
Glyphyalinia indentata	8	26	237	4.1	9	9	*
Punctum minutissimum	9	25	323	5.6	8	8	*
Pupoides albilabris	10	24	311	5.4	9	9	*
Vallonia parvula	11	22	489	8.4	7	7	*
Gastrocopta procera	12	22	165	2.8	7	7	*
Zonitoides arboreus	13	20	79	1.4	7	6	
Succineidae	14	17	78	1.3	7	2	
Helicodiscus singleyanus	15	14	115	2.0	6	6	*
Gastrocopta corticaria	16	10	29	0.5	7	7	*
Euconulus fulvus	17	7	14	0.2	4	4	
Anguispira alternata	18	6	56	1.0	4	2	
Vallonia perspectiva	19	4	7	0.1	3	3	
Vallonia costata	20	2	74	1.3	1	1	
Strobilops affinis	21	2	14	0.2	1	1	
Stenotrema barbatum	22	2	3	<0.1	2	2	
Deroceras laeve	23	2	2	<0.1	2	2	*
Vallonia pulchella	24	1	6	<0.1	1	1	
Cochlicopa lubrica	25	1	5	<0.1	1	1	
Striatura milium	26	1	4	<0.1	1	1	
Mesodon clausus	27	1	1	<0.1	1	0	
Nesovitrea electrina	28	1	1	<0.1	1	1	
Columella edentula	29	1	1	<0.1	1	0	
Taxa not included:							
Vallonia sp. [Juveniles]		24	1,194				
Strobilops sp. [Juveniles]		18	365				
Striatura sp. [Juveniles]		1	1				
Juveniles [undefined taxa]		33	1,313				

frost-free period northward along the valley corridor. Hill prairies along this corridor are the only known modern locations in Wisconsin supporting *Gastrocopta procera* populations.

The large number of state and county records established during this baseline survey indicates the lack of prior study on the small-sized snail fauna in western Wisconsin. At least one species, *Gastrocopta procera*, now classified as Threatened in Wisconsin, is believed to represent a relict population from the mid-Holocene warm/dry Atlantic climatic episode. The land snail faunas of western Wisconsin's hill prairies are only one component of a complex community of animals and plants associated with this striking landscape (Imlay, 1973). The continued existence in Wisconsin of *Gastrocopta procera*, and perhaps of other members of this biotic community, depends on the continued existence of the hill prairie habitats.

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Table 5. Terrestrial gastropods recovered from nine high-stress habitats in western Wisconsin.

County:	Grant		Lafayette	Crawford			Vernon		
Sample Location:	Dewey Hts.		M-Mound	Rush Creek			Cedar Valley		
UWV	3050	3052	3038	3032	3033	3034	3027	3028	3039
Taxon: Sample volume:	1.0	1.2	NR	0.5	0.1	0.4	2.0	0.6	NR
Euconulus fulvus	—	—	—	—	—	—	9	—	—
Glyphyalinia indentata	3	—	—	—	—	—	—	—	—
Hawaiia minuscula	—	—	—	1	—	—	—	—	—
Zonitoides arboreus	1	—	—	—	—	—	2	—	4
Anguispira alternata	—	—	27	—	—	—	—	—	—
Helicodiscus parallelus	4	1	—	2	—	—	—	—	—
Helicodiscus singleyanus	1	—	—	—	—	—	—	—	—
Punctum minutissimum	—	1	—	—	—	—	—	—	—
Succineidae	—	—	—	—	—	—	6	1	3
Strobilops labyrinthica	1	—	—	—	—	—	—	—	5
Strobilops affinis	—	—	—	—	—	—	—	—	1
Strobilops sp.	2	—	—	—	—	—	—	—	2
Gastrocopta armifera	96	98	37	15	—	13	39	5	77
Gastrocopta contracta	—	—	—	—	—	—	—	1	11
Gastrocopta holzingeri	4	74	—	24	—	—	—	—	1
Gastrocopta pentodon	3	—	—	—	—	—	—	3	2
Gastrocopta corticaria	47	1	6	2	13	1	26	2	120
Pupoides albilabris	13	—	—	—	—	—	—	—	3
Vallonia costata	—	—	—	5	—	8	51	13	120
Vallonia parvula	—	2	—	1	—	—	—	—	—
Vallonia perspectiva	40	38	158	—	—	—	5	1	2
Vallonia sp.	83	86	265	9	1	4	118	33	15
Juveniles	127	76	38	19	12	12	51	14	15

NR = Not recorded.

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Table 6. Rank order and assemblage frequency of summed terrestrial gastropods from nine high-stress habitats in western Wisconsin.

Species	Rank	Number of assemblages in which species occurred	Number of specimens	%
Gastrocopta corticaria	1	9	218	17.4
Gastrocopta armifera	2	8	380	30.3
Vallonia perspectiva	3	6	244	19.5
Vallonia costata	4	5	197	15.7
Gastrocopta holzingeri	5	4	103	8.2
Succineidae	6	3	10	0.8
Gastrocopta pentodon	7	3	8	0.6
Zonitoides arboreus	8	3	7	0.6
Helicodiscus parallelus	9	3	7	0.6
Vallonia parvula	10	3	3	0.2
Pupoides albilabris	11	2	16	1.3
Gastrocopta contracta	12	2	12	1.0
Strobilops labyrinthica	13	2	6	0.5
Anguispira alternata	14	1	27	2.2
Euconulus fulvus	15	1	9	0.7
Glyphyalinia indentata	16	1	3	0.2
Hawaiia minuscula	17	1	1	0.1
Helicodiscus singleyanus	18	1	1	0.1
Punctum minutissimum	19	1	1	0.1
Strobilops affinis	20	1	1	0.1
Taxa not included:				
Vallonia sp. [Juveniles]		9	614	
Strobilops sp. [Juveniles]		2	4	
Juveniles [undefined taxa]		9	364	

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A New Gastropod Fauna From An Oligocene Back-Reef Lagoonal Environment In West Central Florida

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ABSTRACT

Twenty-one new species of gastropods and three new gastropod genera are described from a newly-recognized back-reef lagoonal facies of the Oligocene Suwannee Formation. The new species, which were collected in a limestone quarry in westernmost Polk County, Florida, include: *Astraea (Astralium) polkensis* n. sp. (Turbinidae), *Pyrazisinus kendrewi* n. sp. (Potamididae), *Prismacerithium prisma* n. sp. (Cerithiidae), *Pachycrommium dalli* n. sp. and *Pachycrommium mansfieldi* n. sp. (both Naticidae), *Cypracorbis kendrewi* n. sp. (Cypraeidae), *Spinifulgur gemmulatum* n. sp. (Busyconidae), *Solenosteira suwanneensis* n. sp. (Buccinidae), *Vasum suwanneensis* n. sp. (Turbinellidae), *Falsilyria kendrewi* n. sp. (Volutidae), *Conomitra kendrewi* n. sp. (Volutomitridae), *Dentimargo dalli* n. sp., *Persicula dockeryi* n. sp., *Persicula macneili* n. sp., *Persicula suwanneensis*, n. sp., *Prunum cricae* n. sp., *Prunum jessicae* n. sp., *Prunum sandrae* n. sp. (all Marginellidae), *Conus (Asprella) kendrewi* n. sp. (Conidae), *Pleurofusia dowlingi* n. sp. (Turridae), and *Suwanneescapha lindae* n. sp. (Cylichnidae). The new genera, which appear to be restricted to Oligocene coralline environments, include: *Cestumcerithium* n. gen. and *Prismacerithium* n. gen. (Cerithiidae) and *Suwanneescapha* n. gen. (Cylichnidae). In total, seventy-two species of gastropods were collected from four different back-reef lagoonal biotopes, including biohermsof the branching coral *Stylophora minutissima*, open-bottom sand areas, sea grass beds, and intertidal mud flats with oyster bars.

Key words: Oligocene, Florida, Suwannee Formation, Coral Bioherm, Gastropoda.

INTRODUCTION

The early Oligocene (Latdorfian) gastropod fauna of the lower Mississippi River Valley and southeastern United States has long been known to be one of the most species-rich in the Eastern North American Cenozoic. This tropical-subtropical fauna is of particular interest to evolutionary paleontologists and biogeographers in that it contains the first-known examples of many classic Neogene Eastern American endemic genera and is the ancestor of the Miocene, Pliocene, and Pleistocene Caloosahatchian Molluscan Provinces (Petuch, 1982; 1988). As presently understood, the richest and best-preserved Oligocene assemblages are found only in southwestern Mississippi State (MacNeil & Dockery, 1984), and this area is considered the archetype for the early Oligocene. To date, three hundred and ninety-seven species and subspecies of gastropods are known from the Vicksburg Group (MacNeil & Dockery, 1984).

In the early part of the Twentieth Century, Vicksburg-aged gastropod faunas were discovered along the Flint River and Blue Springs areas near Bainbridge, Georgia (Dall, 1916). These were found to be associated with the rich and extensive Oligocene coral reefs that were described from the same area by Vaughan (1900). Later, Mansfield (1937) described an even richer Floridian Vicksburg-aged gastropod fauna, primarily from quarries in Pasco and Hernando Counties (west central Florida) and showed that several Flint River species occurred that far south. Although containing some elements of the classic Vicksburg fauna of the Mississippi Embayment, these two southern coral reef-associated faunas also housed numerous characteristic endemic elements, including the strombid *Orthaulax*, the volutid *Falsilyria*, and a distinctive assemblage of over fifteen species of cerithiids and five potamidids (combined Flint River and Suwannee Formations). Since Mansfield's work in 1937, however, no new comprehensive study of the systematics of the Suwannee gastropods has been published.

Recently, an exposure of a previously-unknown, highly fossiliferous facies of the Suwannee Formation has been found in a limestone quarry in extreme western Polk County, west central Florida (The Terramar Pit on Florida Highway 54, approximately 5 miles east of Zephyrhills, Pasco County) (E. Vokes, 1992). This locality rep-

resented a back-reef lagoonal environment that had formed behind a reef tract to the west and contained the largest number of gastropod species yet found at any single Suwannee exposure. All specimens of corals and mollusks from the Terramar site are silicified (siliceous pseudomorphs), much like the Flint River material, and are generally well-preserved. Through the intensive collecting of Mr. Eric Kendrew of Valrico, Florida, and through additional collecting by myself, seventy-two species of gastropods (listed in Appendix 1) are now known from the Terramar Pit, more than doubling Mansfield's total of thirty-one species. Nine of the Suwannee species reported by Mansfield (1937) and one by E. Vokes (1992) were not collected at the Terramar site, and these are listed in Appendix 2. When Mansfield's and Vokes' additional species are combined with the list of those from the back-reef lagoonal environment, the total number of known Suwannee gastropods increases to eighty-two, less than one third of the number of Vicksburg species.

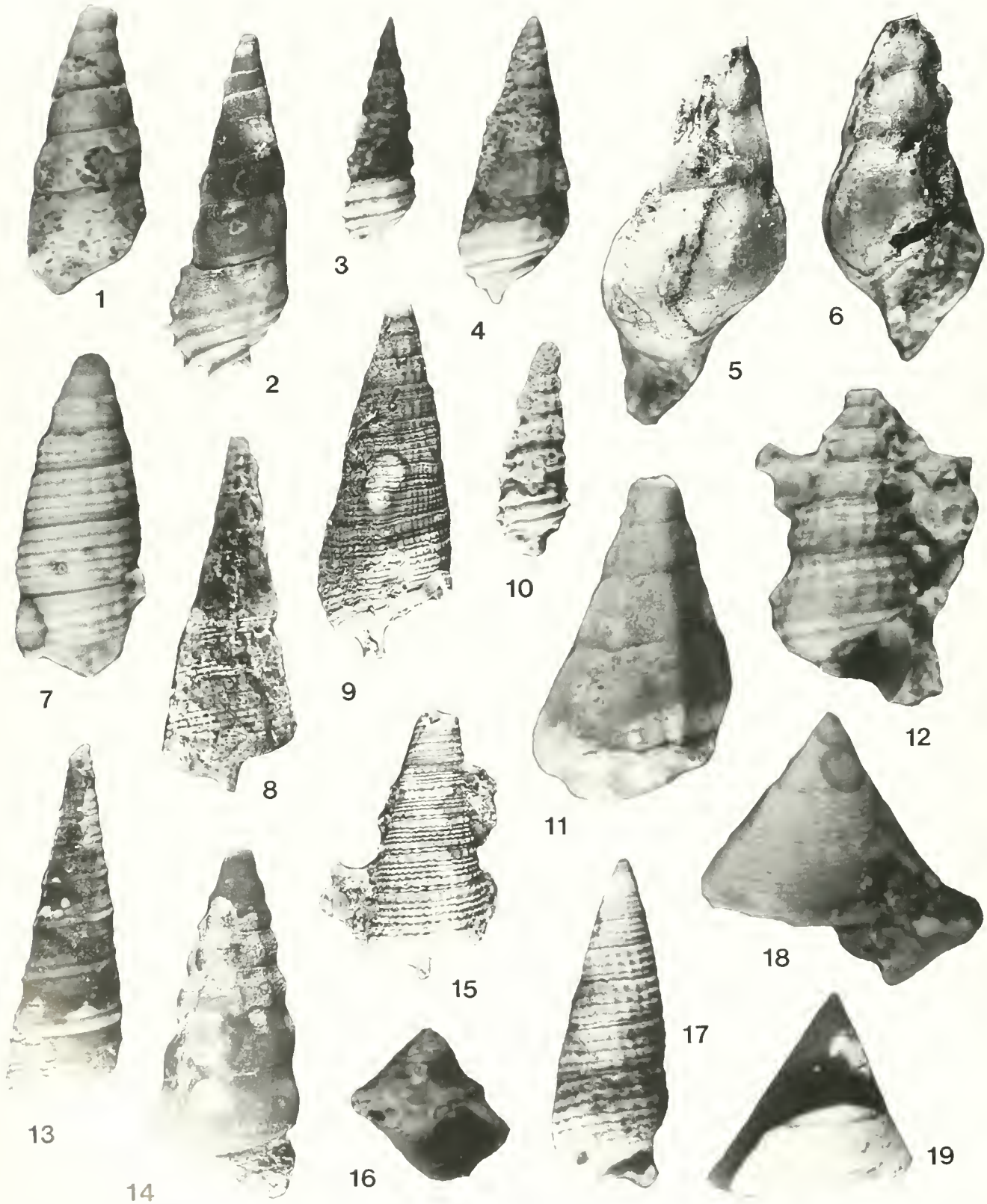
Of the seventy-two species collected at the Terramar Pit, twenty-one are new to science. Three new genera, all of which appear to be endemic to the coralline environments of the Flint River and Suwannee Formations, are also new. Following a discussion of the paleoecology of the Terramar Oligocene site, these new species and genera are described.

PALEOECOLOGY OF THE BACK-REEF LAGOONAL ENVIRONMENT OF THE SUWANNEE FORMATION

The study material from the Terramar Pit was collected either as perfectly-preserved specimens loosely embedded in a residual unconsolidated calcilutite or as specimens embedded in blocks of a dense, partially-silicified limestone. These specimens were often removed in a fragmentary state. Judging from the biotic assemblage collected in both lithofacies, the entire area represented a shallow (less than 5m depth), quiet-water carbonate lagoon. This lagoon formed behind a still-unstudied coral reef tract that had developed farther to the west. Evidence for this unmapped Oligocene reef tract, including the presence of massive coral heads and reef mollusks such as the bivalves *Lima halensis* Dall, 1916 and *Chama* sp. and the stromboidean gastropod *Terebellum hernandoensis* Mansfield, 1937, has been uncovered in quarries in central Pasco and Hernando Counties (Mansfield, 1937). The Terramar lagoonal environment, existing between this reef tract and the Oligocene western coast of Florida, contained four main substrate types: 1. bioherms composed of *Stylophora* corals; 2. deeper lagoonal, open-bottom areas; 3. sea grass beds, and; 4 very shallow-water oyster beds and intertidal mud flats.

Of the four biotopes that existed within the Terramar back-reef lagoon, that of the *Stylophora* coral bioherms was apparently the most extensive. Composed almost entirely of the small branching coral *Stylophora minutissima* Vaughan, 1900 these bioherms formed densely intermeshed beds that sheltered a wide variety of gastropods. Many blocks of limestone examined contained literally hundreds of small pieces of this branching coral and loose fragments were the most abundant component of the residuum facies. As evidenced by having been collected *in situ* in *Stylophora*-rich limestone blocks, a number of Suwannee endemic mollusks appear to have been associated with these bioherms. Some of the most characteristic gastropods include *Calliostoma silicatum* Mansfield, 1937 (figure 19) *Cypraecorbis kendrewi* n. sp. (figures 22, 23), *Solenosteira suwanneensis* n. sp. (figures 33, 34), *Vasum suwanneensis* n. sp. (figures 48, 49), *Falsilyria kendrewi* n. sp. (figures 37, 38), and *Conus (Asprella) kendrewi* n. sp. (figure 72). Several of the large Suwannee cerithiids, including *Cestumcerithium brooksvillensis* (Mansfield, 1937)(figures 3, 10) *Cestumcerithium pascoensis* (Mansfield, 1937)(figure 2), and *Prismacerithium prisma* n. sp. (figures 5, 6, 11) were also associated with the *Stylophora* bioherms. Interestingly, several specimens of *Pachycrommium mansfieldi* n. sp. (figure 30) were also collected in *Stylophora*-rich limestone, possibly indicating that this naticid may have lived on, or in close proximity to, the coral bioherms. The rare muricid *Poirieria (Dallimurex) rufirupicolus* (Dall, 1916) (figure 31), which was previously known only as an internal mold from the Flint River Formation, was also found to be associated with this biotope. Small heads of the star corals *Montastrea bainbridgensis* (Vaughan, 1919) and *Antiguastrea silicensis* Vaughan, 1919 were also present, although uncommonly, throughout the *Stylophora* bioherms.

Interspersed between the coral bioherms in deeper water (approximately 4–5 m) areas were large patches of open, fine-grained carbonate sand bottom. This biotope supported a rich gastropod fauna of which the Suwannee endemics *Oliva (Omogymna) brooksvillensis* (Mansfield, 1937) (figure 65) and *Apicula bowenae* (Mansfield, 1937) (figure 13) were the most abundant. A large Vicksburg-aged marginellid fauna also was associated with this biotope, and included species such as *Persicula dockeryi* n. sp. (figures 52,53), *Prunum cricae* n. sp. (figure 64), *Prunum jessicae* n. sp. (figures 56, 57), and *Prunum sandrae* n.sp. (figures 58, 59). The strombid *Orthaulax hernandoensis* Mansfield, 1937 (figures 20, 21) which is also present in the coral reef environments of the Flint River Formation, was abundant on these open bottom areas, living in large colonies much like *Strombus* s.s. species do in the Recent. Several of the new Suwannee species described here, such as *Pachycrommium dalli* n. sp. (figure 26), *Spinifulgur gemmulatum* n. sp. (figure 47), *Conomitra kendrewi* n. sp.(figures 44, 45) and *Pleurofusia doulingi* n. sp. (figure 68) also appear to be associated with this biotope. All of the widespread Vicksburgian gastropods found in the Terramar Pit (Appendix 1, designated by the letter "V"), including such characteristic species as *Semivertagus mcnthafontis* MacNeil, 1984 (figure 7), *Ficus mississippiensis* Conrad, 1848 (figure 24), *Talityphis mississippiensis* (Gertmann, 1969)(figure 29), *Pallacera caseyi* (MacNeil, 1848), *Clavolithes vicks-*



Figures 1–19. Trochidae, Turbinidae, Potamididae, Cerithiidae, and Modulidae from the Suwannee back-reef lagoons. **1.** *Cerithium* (new genus?) *cooke*i Dall, 1916, length 36 mm. **2.** *Cestumcerithium pascoensis* (Mansfield, 1937), smooth variant, length 37 mm, type of the new genus *Cestumcerithium*. **3.** *Cestumcerithium brooksvillensis* (Mansfield, 1937), length 24 mm. **4.** *Cestumcerithium lit coakensis* (Mansfield, 1937), length 24 mm. **5,6.** *Prismacerithium prisma* Petuch, n.sp., holotype (UF 75978)(fragmentary, missing

burgensis (Conrad, 1848)(figure 46), *Fusimitra conquista* (Conrad, 1848)(figure 50), and *Terebra(Terebrellina) divisura* Conrad, 1848, were associated with this open-bottom area. The Flint River species *Semivertagus silicium* (Dall, 1916)(figure 17), *Cerithium* (new genus?) *cookei* Dall, 1916 (figure 1), *Ampullinopsis flintensis* (Mansfield, 1937) (figure 25), and *Falsilyria mansfieldi* (Dall, 1916)(figures 39,40), also occurred in this biotope. The classic Suwannee index echinoid *Rhyncholampas gouldii* (Bouvé) was abundant on these open-bottom areas and may have been preyed-upon by the widespread Vicksburgian *Phalium caelatura* (Conrad, 1848)(figure 27).

Also interspersed between the large *Stylophora* bioherms were beds of sea grass, most probably *Thalassia*. Evidence for these *Thalassia* beds is seen in the presence of characteristic indicator gastropods, all of which have *Thalassia*-dwelling descendants in the Recent. Living on the sea grass blades were a number of small algivorous species, including *Astraea (Astralium) polkensis* n. sp. (figure 18), *Cerithium insulatum* Dall, 1916, (figure 12) and *Modulus liveoakensis* Mansfield, 1937 (figure 16), and a large fauna of small, *Thalassia*-loving marginellids such as *Dentimargo dalli* n. sp. (figures 62,63), *Hyalina silicifluvia* (Dall, 1916)(figure 51), *Persicula mueneili* n. sp. (figures 54,55), and *Persicula suwanneensis* n. sp. (figures 60,61). Living within the grass beds were larger gastropods such as *Cerithioclava cutextile* (Dall, 1916)(figure 9), the Suwannee endemic *Turbinella suwanneensis* (Mansfield, 1937)(figure 42, 43), and a host of small bivalves, primarily *Chione bainbridgensis* Dall, 1916, *Phacoides hernandoensis* Mansfield, 1937, and *Glycymeris suwanneensis* Mansfield, 1937. A living analogue to the Suwannee grass bed community is seen in the Recent along Roatan Island, Honduras, where species of *Cerithioclava*, *Turbinella*, *Astraea*, *Modulus*, *Persicula*, *Hyalina*, and *Phacoides* all co-occur in *Thalassia* beds. The unusual Suwannee endemic bubble shell, *Suwanneescapha lindae* n. sp. (figures 70,71), may also have been associated with the sea grass beds.

Faunal evidence also points to the existence of shallow intertidal mud flat environments within the Terramar lagoon system. This is seen in the presence of a distinctive potamidid fauna composed of two species of *Telescopium*, [*T. blackwaterensis* (Mansfield, 1937) figure 15, and *T. hernandoensis* (Mansfield, 1937) figure 8], and *Pyrazisinus kendrewi* n. sp. (figure 14). In the Recent Indo-Malaysian region, the amphibious genus *Telescopium* lives on the highest mud flat areas near mangroves and is exposed to air for long periods of time. Often living along with *Telescopium* on these exposed flats is the genus *Terebralia*, which is closely related to the Floridian endemic genus *Pyrazisinus* and probably occupies the same ecological niche as did its extinct New World counterpart. The oyster *Ostrea paroxis* (Lesueur) Dockery, 1984 is commonly encountered in large masses in some blocks of limestone, indicating that small oyster bars also grew on these intertidal mud flats. The melongenid *Myristica crassicornuta* (Conrad, 1848)(figures 35, 36) and the muricid *Pterynotus propeposti* (Mansfield, 1937)(figure 64) were associated with these oyster bars and were probably the major predators on *Ostrea paroxis*. A Recent analogue to this Oligocene mud flat and oyster bar environment is seen in northwestern Australia along the Arafura Sea, where *Pterynotus (Rhednalli)*, *Terebralia*, and *Telescopium* species occur together on mud flats and oyster bars near mangrove forests.

SYSTEMATIC SECTION

The holotypes of the new species described here are deposited in the fossil invertebrate collection of the Florida Museum of Natural History, University of Florida, Gainesville, Florida, and bear UF numbers. Paratypes are deposited in the research collection of the author, as is a voucher collection of each species collected at the Terramar site. All specimens are siliceous pseudomorphs. A voucher collection is also deposited at the Graves Museum of Archaeology and Natural History, Dania, Florida.

Class Gastropoda
Superfamily Trochoidea
Family Turbinidae
Subfamily Astraeinae
Genus *Astraea* Röding, 1798
Subgenus *Astralium* Link, 1807
Astraea (Astralium) polkensis new species
(figure 18)

Description: Shell small for genus and subgenus, conical, with elevated spire whorls; suture indistinct; periphery of body whorl flattened, bladelike, rounded, with faint serrations; peripheries of early whorls and spire whorls edged with 15–20 small, rounded knobs; whorls strongly ornamented with 5 strong, beaded spiral cords;

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approximately one-half of spire whorls), length 45 mm. (type of the new genus *Prismacerithium*). **7.** *Semivertagus mouthafontis* MacNeil, 1984, length 15 mm. **8.** *Telescopium hernandoensis* (Mansfield, 1937), length 49 mm. **9.** *Cerithioclava cutextile* (Dall, 1916), length 57 mm. **10.** *Cestumcerithium brooksvillensis* (Mansfield, 1937), heavily-sculptured variant, length 29 mm. **11.** *Prismacerithium prisma* Petuch, n.sp., paratype (spire whorls, missing part of body whorl), length 19 mm. **12.** *Cerithium (Thericium) insulatum* Dall, 1916, length 22 mm. **13.** *Apicula bowenae* (Mansfield, 1937), length 39 mm. **14.** *Pyrazisinus kendrewi* Petuch, n.sp., holotype (UF 75977), length 62 mm. **15.** *Telescopium blackwaterensis* (Mansfield, 1937), length 43 mm. **16.** *Modulus liveoakensis* Mansfield, 1937, height 15 mm. **17.** *Semivertagus silicium* (Dall, 1916), length 15 mm. **18.** *Astraea (Astralium) polkensis* Petuch, n.sp., holotype (UF 75976), height 11 mm. **19.** *Calliostoma silicatum* Mansfield, 1937, height 14 mm.

1 to 3 extremely fine, threadlike secondary spiral cords present between 5 main cords; base of shell flattened, ornamented with 10 strong spiral cords; umbilical region slightly depressed.

Material examined: HOLOTYPE—Height 11 mm, diameter (incomplete) 13 mm, in back-reef lagoonal facies of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF 75976.

Etymology: Named for Polk County, Florida, locality of the Terramar Pit.

Discussion: This new species is the first *Astraea* known from the Eastern North American Oligocene. Of the known Cenozoic American *Astralium* species, *A. polkensis* is closest to the late Eocene (Jackson Stage) *Astraea* (*Astralium*) *withlacoochensis* Palmer, 1953 from the Inglis Formation of the Floridian Ocala Group. The new species differs from this probable Eocene ancestor in having a smaller shell with a flatter, less trochiform shape, stronger spiral sculpture on the whorls, and a reduced, nonprominent peripheral keel.

Superfamily Cerithioidea
Family Potamididae
Genus *Pyrazisinus* Heilprin, 1886
Pyrazisinus kendrewi new species
(figure 14)

Description: Shell of average size for genus, elongated, cerithiform; whorls ornamented with large, prominent, evenly-spaced knobs; knobs distinctly angled at shoulder, averaging 10 per whorl; whorls sculptured with 5 large, prominent, raised spiral cords; base of shell flattened; suture impressed, slightly canaliculate; apertural region of unique holotype broken, so exact nature of adult lip is not known.

Material examined: HOLOTYPE—Length 62 mm, width 28 mm, in mud flat and oyster bar facies of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF 75977.

Etymology: Named for Mr. Eric Kendrew of Valrico, Florida, who collected the holotype in the Terramar Pit.

Discussion: *Pyrazisinus kendrewi* is the oldest-known member of its endemic Floridian genus. The new species is most similar to the Aquitanian Miocene *P. cornutus* (Heilprin, 1886) from the Tampa Member of the Arcadia Formation, but differs in being a narrower more elongated shell with more numerous knobs per whorl, in having an angled shoulder area and angled knobs, and in having a much more sculptured shell, with five distinct spiral cords.

Family Cerithiidae

Genus *Cestumcerithium* new genus

Diagnosis: Cerith shells of average-to-large size (25–45 mm), slender and elongated; sutures indented, producing turreted spire whorls; shell sculpture characteristically composed of two distinct sections, with early whorls having a reticulate sculpture composed of strong, often beaded, spiral cords intersected by longitudinal ribs, and with the later whorls and body whorl being smooth, with five or six very large, very prominent belt-like spiral cords; on adults, belt-like cords extend beyond edge of lip, producing strong dentate, serrated appearance (shown here in figure 2); siphonal canal short, stubby.

Type species: *Cerithium pascoensis* Mansfield, 1937, Suwannee Formation, early Oligocene of Florida (figure 2).

Other species in *Cestumcerithium*: *Cerithium brooksi illensis* Mansfield, 1937 (figures 3,10), *Cerithium liveoakensis* Mansfield, 1937 (figure 4), and *Cerithium suwanneensis* Mansfield, 1937, all from the Suwannee Formation, early Oligocene of Florida, and *Cerithium vaginatum* Dall, 1916, Flint River Formation, early Oligocene of southern Georgia and Alabama, and the Suwannee Formation of Florida.

Etymology: A combination of the Latinized Greek "*cestus*" (belt) and "*Cerithium*" (little horn), producing "belted little horn", in reference to the prominent and characteristic cords on the body whorl.

Discussion: With the exception of the Flint River and Suwannee *Cestumcerithium vaginatum*, all other known species of this new genus have been found only in the Floridian Oligocene. Here, they appear to have been closely associated with the extensive coral reefs and coral bioherms that dominated Latdorfian western Florida. Four of the five known species are restricted to the Suwannee Formation and can be considered classic index fossils for the Floridian early Oligocene. The genus appears to have been restricted to the Oligocene, as no known members have been collected in the overlying Tampa Member of the Arcadia Formation (Aquitanian Miocene) or from the underlying Eocene formations.

The amount and degree of the characteristic belt-like corded sculpture appears to be variable, sometimes covering only the last two whorls and at other times covering most of the later whorls of members of the same species. This is particularly noticeable on the type species, *Cestumcerithium pascoensis*, which can be heavily belted (like the holotype, Mansfield, 1937, plate 7, figure 4) or relatively smooth, with only the body whorl being belted (like the specimen illustrated here in figure 2, or like Mansfield's "*Cerithium* sp. aff. *vaginatum* Dall", plate 8, figure 4). Specimens of *C. pascoensis* with belted sculpture that intergrades between these two morphological extremes have been collected at the Terramar Pit, demonstrating their conspecificity. This same degree of sculptural variability is also seen in *C. brooksi illensis*, with some specimens having at least half the whorls belted (like figure 10 shown here or like Mansfield's (1937) figure 3 on plate 7) and others having the belted sculp-

ture only on the body whorl (like figure 3 shown here or like Mansfield's figure 5 on plate 7).

Cestumcerithium is most similar to the sympatric genus *Thericium* but differs in having the body whorl, and sometimes the later whorls, sculptured with the prominent beltlike cords and in having a strongly dentate edge to the adult lip.

Genus *Prismacerithium* new genus

Diagnosis: Cerith shells of large size, averaging 60 mm in length, elongatedly pyramidal in outline; shells highly inflated, extremely thin and fragile; shoulder sloping, suture impressed, producing turreted spire whorls; whorls ornamented with 8 low, evenly-spaced narrow axial swellings, producing undulating, faceted appearance; undulating varices become obliquely angled on body whorl; entire shell surface smooth, faintly sculptured with 24–26 extremely fine, evenly-spaced incised spiral threads; aperture oval in shape, with adult lip almost nonexistent, only faintly thickened.

Type species: *Prismacerithium prisma* Petuch, n.sp., Suwannee Formation, early Oligocene of Florida (figures 5,6,11).

Etymology: A combination of the Latinized Greek "*prisma*" (sawed or faceted) and "*Cerithium*" (little horn), in reference to the faceted appearance of the shell whorls.

Discussion: With its large paper thin, highly inflated shell and faceted appearance, *Prismacerithium* stands out as one of the most distinctive members of the rich cerithiid fauna of the Suwannee coral reefs. Because of its extreme fragility, this new genus is almost always collected as broken fragments. Judging from the abundance of shattered pieces in the limestone blocks within the Terramar Pit, however, *Prismacerithium* must have been a common component of the *Stylophora* bioherms.

Although having the large size of other Suwannee cerithiid genera such as *Thericium*, *Cerithioclava*, and *Cestumcerithium*, *Prismacerithium* more closely resembles an immensely-oversized *Alaba*. Both genera, although differing greatly in size, share several morphological characteristics, such as the highly inflated, thin shell, distinct rounded axial swellings, and a shell ornamentation of finely incised spiral threads. Further research and larger collections of better specimens may show that *Prismacerithium* belongs, along with *Alaba* and *Alabina*, in the subfamily Diastomatinae.

At present, *Prismacerithium* is known only from the lagoonal facies of the Suwannee Formation. It bears no similarities to any other known large contemporaneous Eastern American cerithiid.

Prismacerithium prisma new species
(figures 5, 6, 11)

Description: General shell shape, form, and size as for description of genus.

Material examined: HOLOTYPE—Length (fragmentary, missing approximately one-half of spire whorls) 45 mm, width 24 mm, in back-reef lagoonal facies (*Stylophora* bioherm) of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF75978; PARATYPE—length (spire whorls missing, part of body whorl 19 mm, same locality as holotype, in the research collection of the author.

Etymology: Named in reference to the faceted appearance of the shell.

Superfamily Naticoidea
Family Naticidae
Subfamily Globulariinae
Genus *Pachycrommium* Woodring, 1928
Pachycrommium dalli new species
(figure 26)

Description: Shell small for genus, elongated, with rounded body whorl and high, stepped, scalariform spire; sutures highly indented, producing wide, shallowly canaliculate subsutural border; edge of canaliculate border slightly raised, faintly carinated; aperture oval; no umbilicus present.

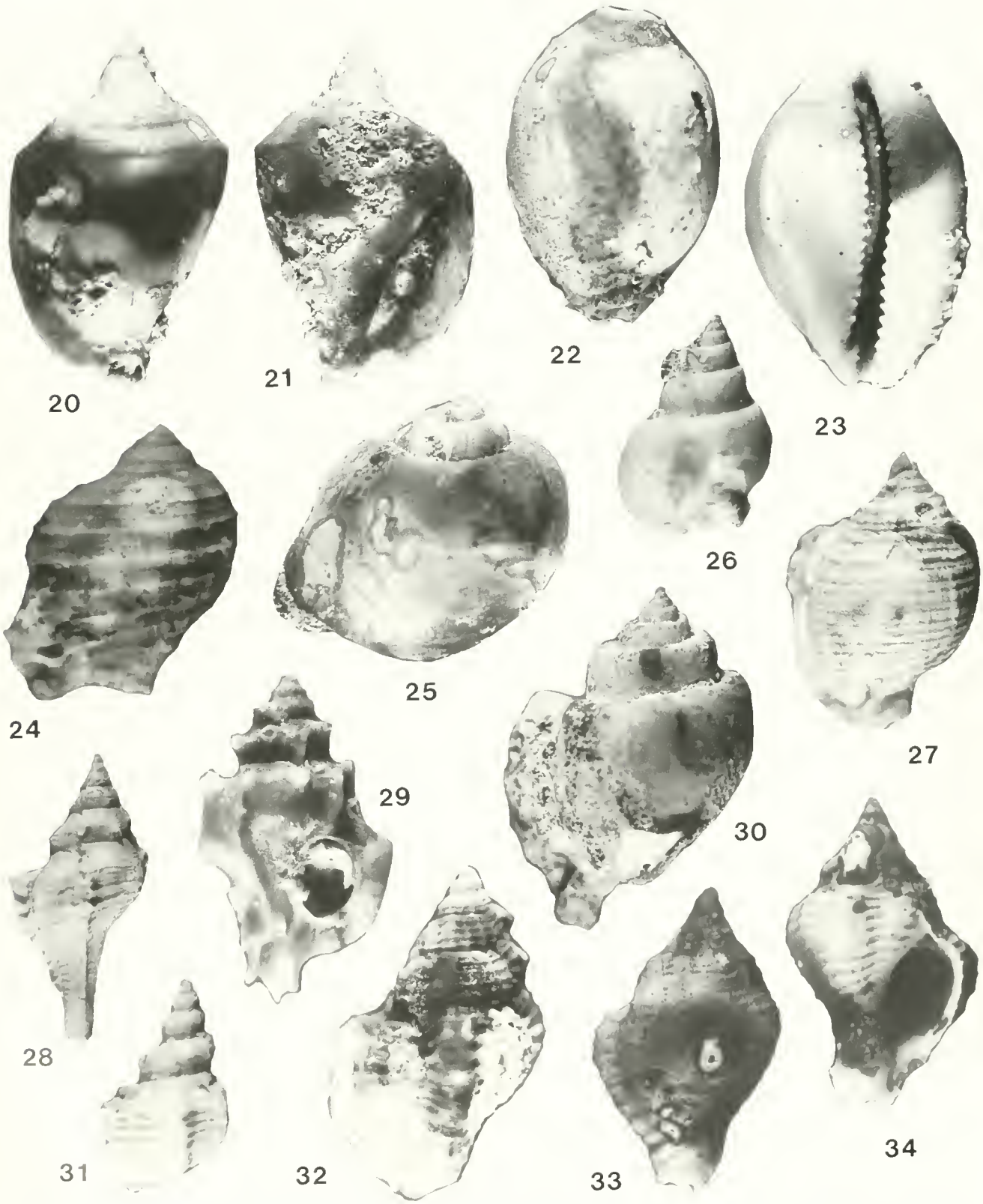
Material examined: HOLOTYPE—Length 18 mm, width 13 mm, in back-reef lagoonal facies of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF 75979

Etymology: Named in honor of the great pioneer paleomalacologist, William Healey Dall, who described the Flint River gastropod fauna.

Discussion: Before its formal description here, this small Oligocene naticid had been illustrated by both Dall (1916, plate 88, fig. 11) and Mansfield (1937, plate 9, fig. 7) but never correctly named. Dall referred it to "*Amauropsis ocalana* Dall", a Jackson-aged Eocene species from the Floridian Ocala Group (a *nomen dubium*—see Mansfield, 1937, p. 177). Mansfield later referred this species to "*Amauropsis* aff. *A. burnsii meridionalis* Pilsbry", a related but different shell from the Miocene Baitoa Formation of the Dominican Republic. Although similar-appearing, both the Eocene and Miocene species differ from *P. dalli* in being larger, more inflated shells with lower, less protracted spires, and in having deeper and wider subsutural channels. To date, *P. dalli* has only been collected in the Flint River and Suwannee Formations.

Pachycrommium mansfieldi new species
(figure 30)

Description: Shell of average size for genus, inflated, globose, with rounded body whorl; spire protracted, scalariform; spire whorls relatively straight-sided; sutures highly indented, producing narrow, very deeply canaliculate subsutural border; edge of canaliculate border



Figures 20–34. Strombidae, Cypraeidae, Ficidae, Cassidae, Naticidae, Muricidae, and Buccinidae from the Suwannee back-reef lagoons. **20,21.** *Orthaulax hernandoensis* Mansfield, 1937, length 70 mm. **22,23.** *Cypracorbis kendrewi* Petuch, n.sp., holotype (UF 75981), length 26 mm. **24.** *Ficus mississippiensis* Conrad, 1848, length 17 mm (fragmentary). **25.** *Ampullinopsis flintensis* (Mansfield, 1937), length 27 mm. **26.** *Pachycrommium dalli* Petuch, n.sp., holotype (UF 75979), length 18 mm. **27.** *Phalium caelatura* (Conrad, 1848), length 29 mm. **28.** *Pterynotus propeposti* (Mansfield, 1937), length 35 mm. **29.** *Talityphis mississippiensis*

highly raised, producing sharp, distinct carina; aperture oval; no umbilicus present.

Material examined: HOLOTYPE—Length 27 mm, width 21 mm, in back-reef lagoonal facies (in association with *Stylophora* bioherms?) of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF75980; PARATYPE—length 24 mm, same locality as holotype, in the research collection of the author.

Etymology: Named in honor of Wendell C. Mansfield, the pioneer paleomalacologist who first described the Suwannee gastropod fauna.

Discussion: This new *Pachycrommium* closely resembles, and is probably ancestral to, *P. floridana* (Dall, 1892) from the Aquitanian Miocene Tampa Member of the Arcadia Formation. The new species differs from *P. floridana* in having a less-inflated shell with straighter sides to the whorls, a more protracted spire, and a much wider and deeper subsutural channel. At present, *P. mansfieldi* is known only from the coral reef lagoonal facies of the Suwannee Formation.

Superfamily Cypraeoidea
Family Cypraeidae
Subfamily Cypraeorbinae
Genus *Cypraecorbis* Conrad, 1865
Cypraecorbis kendrewi new species
(figures 22, 23)

Description: Shell of average size for genus, ovate, slightly subcylindrical; base flattened; aperture narrow, widening slightly toward anterior end, almost straight, recurving slightly at posterior end; labial teeth proportionally large, extending onto base of lip, 23 in number; columellar teeth smaller than labial teeth, 21 in number; extremities reduced, projecting only slightly from main shell body; spire and posterior extremity covered with broad, low callus; fossula poorly-developed, supported by single large tooth along anterior edge.

Material examined: HOLOTYPE—Length 26 mm, width 18 mm, in back-reef lagoonal facies (*Stylophora* bioherm) of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF75981; Paratype-length 26 mm, same locality as holotype, in the research collection of the author.

Etymology: Named for Mr. Eric Kendrew of Valrico, Florida, who collected the holotype in the Terramar Pit.

Discussion: *Cypraecorbis kendrewi*, one of the last species of the *Cypraecorbis* lineage, is most similar to *C. ventripotens* (Cossmann, 1903) from the Jackson Eocene Moodys Branch Formation of Mississippi. The new species differs from this older cowrie in having a much more cylindrical, less inflated shell with straighter sides, more rounded, less projecting extremities, a straighter, less recurved aperture, and more numerous and finer apertural teeth. The Vicksburg Oligocene cowrie listed as "*Cypraecorbis* aff. *C. ventripotens* (Cossman, 1903)" by MacNeil and Dockery (1984, plate 16, figs. 10,12,15) is very similar to *C. kendrewi*, but differs in being a more inflated, rounded shell with a slightly more recurved aperture. Further study may show that the Mississippi shell (from the Mint Springs Formation) belongs to a northern population of *C. kendrewi*.

Superfamily Buccinoidea
Family Busyconidae
Subfamily Busyconinae
Genus *Spinifulgur* Petuch, 1994
Spinifulgur gemmulatum new species
(figure 47)

Description: Shell of average size for genus, with distinctly sloping shoulders and high pagodiform spire; edge of shoulder sharply angled, bordered by prominent, thick, undulating carina; undulations on carina produce small, rounded, evenly-spaced knobs, numbering between 14 and 18 per whorl; suture highly indented, causing carina on previous whorl to overhang subsequent whorl; sloping spire whorls heavily ornamented with 8 strong spiral threads between which are intercalated very fine secondary threads; body whorl (portion exposed in matrix, just anterior of shoulder carina of holotype) ornamented with 5 (extrapolated from holotype) very large, thick, beaded spiral cords; aperture and siphonal canal unknown.

Material examined: HOLOTYPE—Length (fragmentary, missing portion of body whorl and siphonal canal) 24 mm, width 16 mm, in back-reef lagoonal facies of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF75928; PARATYPE-spire only, width 16 mm, same locality as holotype, in research collection of the author.

Etymology: "Gemmed", in reference to the characteristic gemlike knobs on the shoulder carina.

Discussion: *Spinifulgur gemmulatum*, although known only from fragmentary specimens, is so distinctive that its formal description seems warranted at this time. The new species is similar to slope-shouldered variants of the Vicksburg Oligocene *Spinifulgur spiniger* (Conrad, 1848) (such as the one illustrated by MacNeil

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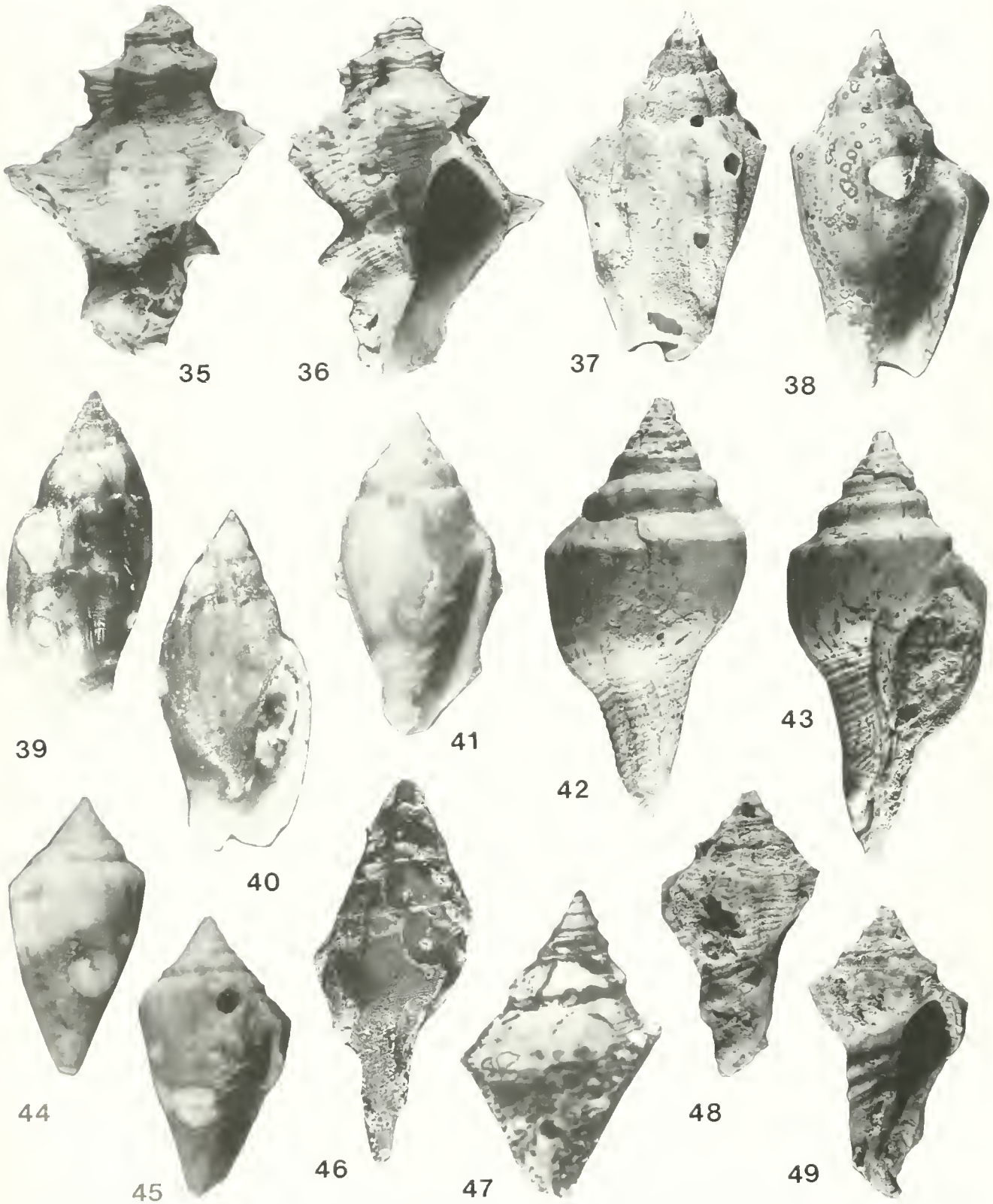
(Gertman, 1969), length 24 mm. **30.** *Pachycrommium mansfieldi* Petuch n.sp., holotype (UF 75980), length 27 mm. **31.** *Poiricria* (*Dallimurex*) *rufirupicolus* (Dall, 1916), fragmentary specimen, length 21 mm (missing portion of body whorl and siphonal canal). **32.** *Chicoreus stetopus* (de Gregorio, 1890), length 32 mm. **33,34.** *Solenosteira suwanneensis* Petuch, n.sp., holotype (UF 75983), length 27 mm.



Figures 35–49. Melongenidae, Busyconidae, Volutidae, Volutomitridae, and Turbinellidae from the Suwannee back-reef lagoons. **35,36.** *Myristica crassicornuta* (Conrad, 1848), length 49 mm. **37,38.** *Falsilyria kendrewi* Petuch, n.sp., holotype (UF 75985), length 37 mm. **39,40.** *Falsilyria mansfieldi* (Dall, 1916), length 32 mm. **41.** *Conomitra crenulata* Dockery, 1984, length 21 mm. **42,43.** *Turbinella suwanneensis* (Mansfield, 1937), length 107 mm. **44,45.** *Conomitra kendrewi* Petuch, n.sp., holotype (UF 75986), length 14 mm. **46.** *Clavilithes vicksburgensis* (Conrad, 1848), length 89 mm. **47.** *Spinifulgur gemmulatum* Petuch, n.sp., holotype

and Dockery, 1984, plate 54, fig.6), but differs in lacking distinct spines, having, instead, low rounded knobs arranged in an undulating pattern. *Spinifulgur gemmulatum* also differs from *S. spiniger* and any other known *Spinifulgur* species, in being heavily sculptured with wide, thick spiral cords on the body whorl. At present, this highly ornate species is known only from the Suwannee Formation.

Family Buccinidae
Subfamily Buccininae
Genus *Solenosteira* Dall, 1890
Solenosteira suwanneensis new species
(figures 33, 34)

Description: Shell of average size for genus, broadly fusiform, inflated, with high, protracted spire; shoulder angled, spire whorls sloping; body whorl with 7–8 very large, rounded, evenly-spaced axial folds; folds become largest at shoulder producing large, rounded knobs at shoulder periphery; suture prominent undulating as it overlaps shoulder knobs of spire whorls; body whorl ornamented with 12 large, raised spiral cords; spire whorls ornamented with 5 spiral cords; siphonal canal well-developed, broad, ornamented with 3 large spiral cords; pseudoumbilicus present, partially covered by parietal shield of siphonal canal; aperture wide, oval in shape.

Material examined: HOLOTYPE—Length 27 mm, width 17 mm, in back-reef lagoonal facies (*Stylophora* bioherm) of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF75984; PARATYPE—length 25 mm, same locality as holotype, in the research collection of the author.

Discussion: *Solenosteira suwanneensis* is the oldest-known member of its genus to be found in Eastern North America. The new species is most similar to *S. inornata* Dall, 1890 from the Aquitanian Miocene Tampa Member of the Arcadia Formation, but differs in having a lower, less protracted spire, in having a much coarser shell sculpture composed of strong spiral cords, and in having more numerous and smaller axial folds and shoulder knobs.

Superfamily Volutoidea
Family Turbinellidae
Subfamily Vasinae
Genus *Vasum* Röding, 1798
Vasum suwanneensis new species
(figures 48, 49)

Description: Shell small for genus, with broad, sharply-angled shoulder; spire stepped, proportionally low, with spire whorls slightly sloping; suture indented, bordered by broad, undulating subsutural collars; shoulder ornamented with 10 large, evenly-spaced, open spines; body whorl sculptured with 8 large primary spiral cords; smaller secondary spiral cords present between some primary cords; spire whorls sculptured with 3 large spiral cords; siphonal canal well developed, ornamented with single row of very large, open spines that correspond to the spacing of the shoulder spines; siphonal canal sculptured with 5 large spiral cords, 2 posterior of row of spines and 3 anterior of spines; aperture open, flaring; columella with 3 very large, prominent plications; on holotype, a fourth very faint plication is present between anterior and medial plications.

Material examined: HOLOTYPE—Length 39 mm, width (fragmentary, missing last third of body whorl) 23 mm, in back-reef lagoonal facies (*Stylophora* bioherm) of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida UF75984.

Etymology: Named for the Suwannee Formation of Florida.

Discussion: *Vasum suwanneensis* is the first known vase shell to be collected in the Eastern American Oligocene. The new species is most similar to *V. humerosum* Vaughan, 1896 from the Jackson Eocene Moodys Branch Formation, but differs in having a lower, flatter spire, in having more numerous primary spiral cords on the body whorl, in having three very large and prominent spiral cords on the spire whorls, and in having a larger, much more prominent, and more elevated subsutural collar. The new species is also similar to *V. subcapitellum* Heilprin, 1886 from the Aquitanian Miocene Tampa Member of the Arcadia Formation, but differs in having a lower, flatter spire, in having finer body whorl sculpture, and in having smaller, stumpier, and less developed shoulder and siphonal spines. As far as is presently known, *V. suwanneensis* was restricted, ecologically, to the coral bioherms of the Floridian Peninsula.

Family Volutidae
Subfamily Volutinae
Genus *Falsilyria* Pilsbry and Olsson, 1954
Falsilyria kendrewi new species
(figures 37, 38)

Description: Shell of average size for genus, fusiform, with high, elevated spire; shoulder, particularly of body whorl and penultimate whorl, sharply-angled, producing distinctly sloping spire whorls; whorls ornamented with 8–10 strong, sharply-angled, evenly-spaced axial ribs; shoulders, particularly of body whorl and penultimate whorls, with 8–10 large, sharp, spinelike knobs, each corresponding to an axial rib; body whorl smooth, with 2–

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(UF 75928) (fragmentary, missing portion of body whorl and siphonal canal), length 24 mm. **48,49.** *Vasum suwanneensis* Petuch, n.sp., holotype (UF 754984), length 39 mm.

Figures 50–72. Mitridae, Margnellidae, Olividae, Conidae, Turridae, and Cylichnidae from the Suwannee back-reef lagoons. **50.** *Fusimitra conquista* (Conrad, 1848), length 35 mm. **51.** *Hyalina silicifluvia* (Dall, 1916), length 12 mm. **52,53.** *Persicula dockeryi* Petuch, n.sp., holotype (UF 75988), length 14 mm. **54,55.** *Persicula macneili* Petuch, n.sp., holotype (UF 75989), length 11 mm. **56,57.** *Prunum jessicae* Petuch, n.sp., holotype (UF 75992), length 16 mm. **58,59.** *Prunum sandrae* Petuch, n.sp., holotype (UF 75993), length 18 mm. **60,61.** *Persicula suwanneensis* Petuch, n.sp., holotype (UF 75990) length 9 mm. **62,63.** *Dentimargo dalli*

3 large spiral cords around anterior end; spire whorls ornamented (particularly on last whorl) with single, large spiral cord; aperture wide, flaring; columella with 5 large, evenly-spaced, beaded plications; protoconch proportionally very small, composed of 2 narrow, smooth whorls.

Material examined: HOLOTYPE—Length 37 mm, width 22 mm, in back-reef lagoonal facies (*Stylophora* bioherm) of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF75985; PARATYPE—length 39 mm, same locality as holotype, in the research collection of the author.

Etymology: Named for Mr. Eric Kendrew of Valrico, Florida, who collected the holotype at the Terramar Pit.

Discussion: *Falsilyria kendrewi* occurs together in the Terramar fauna with *F. mansfieldi* (Dall, 1916) (figures 39, 40), but can be readily distinguished from its better-known congener in having a consistently broader, more inflated, and less elongated shell, with prominent spine-like shoulder knobs, and in being a smoother shell that lacks the spiral cord sculpture on the body whorl. Likewise, two *Falsilyria* species occur together in the reefal environments of the Burdigalian Miocene Chipola Formation. Of these two, *F. mansfieldi* appears to be ancestral to the smooth-shouldered *F. anoptos* Hoerle and Vokes, 1978 while *F. kendrewi* appears to be ancestral to the knobbed-shouldered *F. pycnopleura* (Gardner, 1937). The smooth-shouldered and heavily-corded *F. musicina* (Heilprin, 1886) from the Aquitanian Miocene Tampa Member of the Arcadia Formation is very similar to *F. mansfieldi* and is the most probable descendant species. No *Falsilyria* with strong shoulder knobs has yet been found in the Tampa fauna. At present, *Falsilyria kendrewi* is known only from the Terramar *Stylophora* bioherms.

Family Volutomitridae
Genus *Conomitra* Conrad, 1865
Conomitra kendrewi new species
(figures 44, 45)

Description: Shell small for genus, biconic, with sharply-angled shoulder and proportionally low spire; anterior two-thirds of body whorl smooth, unornamented; spire whorls and posterior one-third of body whorl heavily sculptured with large, evenly spaced rib-like plications, averaging 20 per whorl; aperture narrow; columella with 5 large plications, with the largest at posterior end, becoming smaller toward anterior end; anterior-most tip of siphonal area ornamented with 4–5 impressed spiral threads.

Material examined: HOLOTYPE—Length 14 mm, width 8 mm, in back-reef lagoonal facies of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF75986; PARATYPES—lengths 14 mm and 17 mm, same locality as holotype, in the research collection of the author.

Etymology: Named for Mr. Eric Kendrew of Valrico, Florida, who collected the holotype at the Terramar Pit.

Discussion: This distinctive new Suwannee *Conomitra* species is most similar to the sympatric and widespread Vicksburgian *C. crenulata* Dockery, 1984, but differs in having a much lower spire with a sharply-angled shoulder and cone-shaped appearance. *Conomitra kendrewi* also differs from *C. crenulata* in having shoulder and spire plications that are proportionally larger and fewer in number. In these characters, the new species is also similar to *C. modesta* Dockery, 1984 from the Vicksburg-aged Forest Hill Formation of Mississippi, but differs in having a much lower spire and much more sharply-angled shoulder.

Family Marginellidae
Subfamily Glabellinae
Genus *Dentimargo* Cossmann, 1899
Dentimargo dalli new species
(figures 62, 63)

Description: Shell of average length for genus, slender, with high, elevated spire; suture indented, producing slightly stepped spire whorls; shoulder of body whorl only slightly angled; aperture narrow at posterior end, rapidly expanding and becoming flaring and open at anterior end; columella with 4 large plications; labrum of adult thickened and callused, with smooth inner edge.

Material examined: HOLOTYPE—Length 15 mm, width 8 mm, in back-reef lagoonal facies (sea grass bed) of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF 75987; PARATYPES—2 specimens, both 14 mm, in length, same locality as holotype, in the research collection of the author.

Etymology: Named in honor of William Healey Dall, the foremost pioneer Floridian paleomalacologist.

Discussion: *Dentimargo dalli* is the oldest known member of its genus to be found in the Floridian Cenozoic. The new species is most similar to *D. elegantula*

←

Petuch, n.sp., holotype (UF 75987), length 15 mm; **64.** *Prunum cricae* Petuch, n.sp., holotype (UF 75991), length 11 mm; **65.** *Oliva (Omogymna) brooksvillensis* (Mansfield, 1937), length 19 mm; **66.** *Olivella vicksburgensis* Dockery, 1984, length 10 mm; **67.** *Pleurofusia brooksvillensis* (Mansfield, 1937), length 26 mm; **68.** *Pleurofusia dowlingi* Petuch, n.sp., holotype (UF 75995), length 26 mm; **69.** *Conorbis porcellanus* (Conrad, 1848), length 36 mm; **70.** *Suwanneascapha lindae* Petuch, n.sp., holotype (UF 75996), length 17 mm (type of the new genus *Suwanneascapha*); **71.** *Suwanneascapha lindae* Petuch, n.sp., view of spire of holotype; **72.** *Conus (Asprella) kendrewi* Petuch, n.sp., holotype (UF 75994), length 35 mm.

(Dall, 1890) from the Aquitanian Miocene Tampa Member of the Arcadia Formation, but differs in being a larger, more slender and elongated shell with a more sloping shoulder, and in having a much more protracted, distinctly scalariform spire. At present, *Dentimargo dalli* is known only from the Suwannee Formation.

Genus *Persicula* Schumacher, 1817
Persicula dockeryi new species
(figures 52,53)

Description: Shell large for genus, ovoid, inflated, slightly flattened dorso-ventrally; posterior extremities well-developed, greatly projecting, recurved strongly toward right side of shell; aperture narrow, widening slightly toward anterior end; posterior end of aperture recurved sharply toward right side of shell; spire whorls not visible, buried in thick callus; columella with 5 large plications; labrum thickened, smooth along inner edge; sharp-edged callus present along posterior of columella, forming open canal in sharply-recurved posterior end of aperture.

Material examined: HOLOTYPE—Length 14 mm, width 9 mm, in back-reef lagoonal facies (open sand bottom) of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF 75988.

Etymology: Named in honor of Dr. David T. Dockery III, of the Mississippi State Bureau of Geology, in recognition of his extensive and important contributions to the systematics of the southeastern U.S. Paleogene mollusks.

Discussion: Of the known Paleogene and early Neogene *Persicula* species, *P. dockeryi* is most similar to *P. progravida* (Gardner, 1937) from the Burdigalian Miocene Oak Grove Formation of southern Georgia and northwestern Florida. The new Oligocene species differs from this possible Miocene descendant in being a larger, more elongated shell, in having a far more recurved posterior end of the aperture, and in having much better developed, more conspicuous, and more-projecting posterior extremities. At present, *Persicula dockeryi* is known only from the Suwannee Formation.

Persicula macneili new species
(figures 54, 55)

Description: Shell of average size for genus, elongately ovate, with relatively straight sides; extremities rounded, only faintly produced, not projecting beyond spire; aperture narrow throughout, slightly recurved to right side of shell at posterior end; columella with 5 plications, labrum thickened with smooth inner edge.

Material examined: HOLOTYPE—Length 11m, width 7 mm, in back reef lagoonal facies (sea grass bed?) of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF 75989.

Etymology: Named in honor of Dr. F. Stearns MacNeil, late of the U.S. Geological Survey, in recognition of his important contributions to the systematics of the Vicksburg mollusks.

Discussion: *Persicula macneili* is similar in appearance to *P. halensis* (Dall, 1916) from the contemporaneous Flint River Formation, but differs in being a larger, more elongated shell with distinctly straighter sides. The new species is also similar to the Vicksburgian *P. vicksburgensis* Dockery, 1984 from the Mint Springs Formation of Mississippi, but differs in being a much larger, more elongated shell with a lower and more rounded spire.

Persicula suwanneensis new species
(figures 60, 61)

Description: Shell of average size for genus, extremely elongated and cylindrical, with straight sides; aperture narrow throughout, recurved to right side of shell at extreme posterior end; spire area flattened; posterior extremity on labial side better developed than posterior extremity of columellar side, projecting beyond plane of spire; extreme posteriormost edge of columellar area with thin, sharp-edged blade, producing open posterior canal with labial projection; columella with 5 plications; labrum thickened, with very fine crenulations along inner edge.

Material examined: HOLOTYPE—Length 9 mm, width 3 mm, in back-reef lagoonal facies (sea grass beds?) of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF75990; PARATYPE—length 10 mm, same locality as holotype, in the research collection of the author.

Etymology: Named for the Suwannee Formation of Florida.

Discussion: *Persicula suwanneensis* is the most slender and elongated of all known Oligocene and Miocene *Persicula* species. This new Suwannee marginella is similar only to the sympatric *P. macneili*, but differs in being even narrower and more elongated, in having the posterior end of the aperture being more recurved, and in having the distinctly projecting posterior labial extremity.

Genus *Prunum* Herrmannsen, 1852
Prunum cricae new species
(figure 64)

Description: Shell small for genus, elongately ovate, with high pyramidal spire; shoulder slightly angled; aperture narrow at posterior end, expanding rapidly toward anterior end, becoming wide, flaring, and open; columella distinctly arcuate, with 4 large plications; labrum thickened, smooth along inner edge.

Material examined: HOLOTYPE—Length 11 mm, width 6 mm, in back-reef lagoonal facies (open sand bottom) of the Suwannee Formation, Terramar Pit, west-

ernmost Polk County, Florida, UF75991; PARATYPES—Lengths 8 mm and 9 mm, same locality as holotype, in the research collection of the author.

Etymology: Named for Ms. Erica Kendrew, daughter of Mr. Eric Kendrew, of Valrico, Florida.

Discussion: Of the three *Prunum* species now known from the Suwannee Formation, *P. ericae* is the smallest and most slender in outline. In general size and shape, *P. ericae* is most similar to *P. infecta* (Dall, 1915) from the Aquitanian Miocene Tampa Member of the Arcadia Formation, but differs in being a more slender shell with a wider aperture. The new species may be ancestral to the radiation of small, high-spired *Prunum* species found in the Tampa Member and including such distinctive taxa as *P. infecta*, *P. impagina* (Dall, 1915), *P. posti* (Dall, 1915), and *P. inepta* (Dall, 1890). The small un-named, high-spired *Prunum* illustrated by MacNeil and Dockery (1984, plate 35, figures 4,5, as "*Marginella* sp.?") from the Byram Formation of the Vicksburg Group is similar to *P. ericae* and may be conspecific.

Prunum jessicae new species
(figures 56, 57)

Description: Shell of average size for genus, cylindrical in form, with distinctly angled shoulder; spire high, protracted, slightly scalariform; spire whorls and shoulder of body whorl sloping; aperture narrow, widening only slightly toward anterior end; columella straight, with 4 large plications; labrum (missing on holotype, but present on paratype) slightly thickened, smooth along inner edge.

Material examined: HOLOTYPE—Length 16 mm, width 9 mm, in back-reef lagoonal facies (open sand bottom) of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF75992; PARATYPES—lengths 14 mm and 11 mm (fragmentary), same locality as holotype, in the research collection of the author.

Etymology: Named for Ms. Jessica Kendrew, daughter of Mr. Eric Kendrew, of Valrico, Florida.

Discussion: With its large size and high scalariform spire, *P. jessicae* is the most easily-recognizable of the Suwannee *Prunum* species. The new species is most similar to, and is possibly the ancestor of, the Aquitanian *P. silicata* (Mansfield, 1937) from the Tampa member of the Arcadia Formation. *Prunum jessicae* differs from the early Miocene species in having a more inflated shell with a more-angled shoulder, and a higher, more protracted spire.

Prunum sandrae new species
(figures 58, 59)

Description: Shell of average size for genus, inflated, ovately subcylindrical; shoulder sharply-angled; spire proportionally low; spire whorls slightly sloping; aperture narrow, widening slightly toward anterior end; columella straight, with 4 large plications; labrum thickened, smooth along inner edge.

Material examined: HOLOTYPE—Length 18 mm, width 11 mm, in back-reef lagoonal facies (open sand bottom) of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF75993; PARATYPES—three specimens, lengths 13 mm, 15 mm, and 19 mm, same locality as holotype, in the research collection of the author.

Etymology: Named for Mrs. Sandra Kendrew, wife of Mr. Eric Kendrew, of Valrico, Florida.

Discussion: *Prunum sandrae* is very similar to, and is undoubtedly the ancestor of, the Aquitanian Miocene *P. gregaria* (Dall, 1915) from the Tampa Member of the Arcadia Formation. Both shells have the same large size, low spire, and narrow aperture. The new species differs from its descendant, however, in being consistently a wider and more inflated shell. *Prunum sandrae* appears to be the commonest marginellid in the Suwannee Formation at Terramar.

Superfamily Conoidea
Family Conidae
Genus *Conus* Linnaeus, 1758
Subgenus *Asprella* Schaufuss, 1869
Conus (*Asprella*) *kendrewi* new species
(figure 72)

Description: Shell of average size for subgenus, elongated, tapering, with straight sides; spire flattened, with faintly stepped, slightly projecting whorls; shoulder sharply-angled, bounded by thick, ridgelike carina; carina present on spire whorls, producing depressed scalariform appearance; body whorl heavily sculptured with (on unique holotype) 24 large, evenly-spaced, highly-raised spiral cords; spire whorls ornamented with 3 fine, evenly-spaced spiral threads; aperture straight, narrow.

Material examined: HOLOTYPE—Length 35 mm, width 21 mm, in back-reef lagoonal facies (*Stylophora* bioherm) of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF 75994.

Etymology: Named for Mr. Eric Kendrew of Valrico, Florida, who collected the holotype at the Terramar Pit.

Discussion: *Conus kendrewi*, with its extremely heavy corded body sculpture, wide shoulder carina, and depressed scalariform spire, is the most distinctive cone shell known from the Eastern American Oligocene. The only contemporaneous cone that even remotely resembles this new species is the sympatric Suwannee and Flint River *C.* (*Leptoconus?*) *cookei* Dall, 1916. *Conus kendrewi* differs from this more wide-ranging species in having a much coarser and stronger spiral cord sculpture, in having a distinctly stepped spire, and in having

a prominent shoulder carina that extends beyond the body whorl outline.

Family Turridae
Subfamily Turriculinae
Genus *Pleurofusia* de Gregorio, 1890
Pleurofusia dowlingi new species
(figure 68)

Description: Shell of average size for genus, elongately fusiform, with high, protracted, scalariform spire, rounded body, and thick, elongated siphonal canal; shoulder slightly angled; suture indented; body whorl ornamented with 9 large, thick spiral cords that become thinner toward anterior; siphonal canal ornamented with 10–12 fine, thin spiral cords; suture bounded with single, large spiral cord; sutural cord separated from shoulder spiral cord by wide, depressed gap, producing slightly canaliculate appearance; spire whorls ornamented with 3 large spiral cords; aperture proportionally small, oval in shape.

Material examined: HOLOTYPE—Length 26 mm width, in back-reef facies of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF75993; PARATYPES-lengths 19 mm and 23 mm, same locality as holotype, in the research collection of the author.

Etymology: Named for Mr. William Dowling of Lake Worth, Florida, who assisted me at the Terramar Pit and who collected the holotype.

Discussion: *Pleurofusia dowlingi* occurs together with the congeneric *P. brooksvillensis* (Mansfield, 1937)(figure 67) at the Terramar Pit, but is never as common. The new species differs from the better-known *P. brooksvillensis* in being a consistently more heavily-sculptured shell with coarser and thicker spiral cords, in lacking varical undulations on the spire and body whorl, and in having a much narrower gap between the sutural cord and shoulder cord.

Order Cephalaspidea
Superfamily Cylichnoidea
Family Cylichnidae
Genus *Suwanneescapha* new genus

Diagnosis: Cylichnid bubble shells of greater-than-average size; widely inflated, ovate, very thin and fragile; spire flattened, planar in profile; suture extremely depressed, producing very deep, wide, open channel (see figure 71); edge of shoulder along channel developed into very thin, sharp, erect blade; body whorl smooth, faintly sculptured with extremely numerous, very fine spiral threads; aperture very wide and flaring, oval in shape; apical perforation absent, replaced by raised protoconch; anal notch well-developed, corresponding to raised shoulder blade along spire channel.

Type species: *Suwanneescapha lindae* Petuch, new species, Suwannee Formation, early Oligocene of Florida (figures 70,71). At present, known only from the Terramar Pit, Polk County, Florida.

Etymology: A combination of "Suwannee" and "*scapha*" (barrel).

Discussion: This unusual cylichnid most closely resembles members of the genus *Scaphander* Montfort, 1810, particularly in shape and size, but is immediately separable by possessing the characteristic widely canaliculate spire. In having a flat, channeled spire, *Suwanneescapha* somewhat resembles a giant version of the diminutive cylichnid genus *Acteocina* Gray, 1847, but differs in being a much more inflated, rotund shell and in having a deeper and much wider spire channel. Morphologically, *Suwanneescapha* combines the large size and inflated shell form of *Scaphander* and the flat, channeled spire of *Acteocina*

Suwanneescapha lindae new species
(figures 70, 71)

Description: As for diagnosis of genus.

Material examined: HOLOTYPE—Length 17 mm, width 11 mm, in back-reef lagoonal facies (sea grass beds?) of the Suwannee Formation, Terramar Pit, westernmost Polk County, Florida, UF75996; PARATYPES—lengths 19 mm, and 21 mm, same locality as the holotype, in the research collection of the author.

Etymology: Named for my wife, Linda Joyce Petuch, who stoically watched over our family while I was off exploring the Suwannee Formation.

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APPENDIX 1

Gastropods From The Back-Reef Lagoonal Facies Of The Suwannee Formation In The Terramar Pit, Polk County, Florida. V = Widespread Vicksburgian Species; F = Species Also Known From The Flint River Formation; S = Species Known Only From The Suwannee Formation.

Trochidae
Calliostoma silicatum Mansfield, 1937 S
Turbinidae
Astraea (Astralium) polkensis Petuch, n.sp. S
Potamididae
Pyrazisinus kendrewi Petuch, n.sp. S
Telescopium blackwaterensis (Mansfield, 1937) S
Telescopium hernandoensis (Mansfield, 1937) S
Cerithiidae
Bittium caseyi MacNeil, 1984 V
Cerithioclava cutextile (Dall, 1916) F
Cerithium (Thericium) insulatum Dall, 1916 F
Cerithium (new genus?) *cookei* Dall, 1916 F
Cestumcerithium brooksvillensis (Mansfield, 1937) S
Cestumcerithium liscoakensis (Mansfield, 1937) S
Cestumcerithium pascoensis (Mansfield, 1937) S
Cestumcerithium vaginatum (Dall, 1916) F
Prismacerithium prisma Petuch, n.sp. S
Semivertagus menthafontis MacNeil 1984 V
Semivertagus silicinus (Dall, 1916) F
Modulidae
Modulus liscoakensis Mansfield, 1937 S
Turritellidae
Apicula bowenae (Mansfield, 1937) S
Torcula caseyi (MacNeil, 1984) S
Torcula mississippiensis (Conrad, 1848) V
Crepidulidae
Calyptraea conradi MacNeil, 1984 V
Strombidae
Orthaulax hernandoensis Mansfield, 1937 F
Ficidae
Ficus mississippiensis Conrad, 1848 V
Cassidae
Phalium cadatura (Conrad, 1848) V
Personiidae
Distorsio (Rhysema) crassidens Conrad, 1848 V
Naticidae
Ampullinopsis flintensis (Mansfield, 1937) F
Natica caseyi MacNeil, 1984 V
Pachycrommium dalli Petuch, n.sp. F, S
Pachycrommium mansfieldi Petuch, n.sp. S
Sinum mississippiensis (Conrad, 1848) V
Cypraeidae
Cypraecorbis kendrewi Petuch, n.sp. (V?) S
Muricidae
Chicoreus stetopus (de Gregorio, 1890) V
Poirieria (Dallimurex) rufirupicolus (Dall, 1916) F
Pterynotus propeposti (Mansfield, 1937) S
Talityphis mississippiensis (Gertmann, 1969) V
Busyconidae
Spinifulgur gemmulatum Petuch, n.sp. S
Buccinidae
Pallacera caseyi (MacNeil, 1984) V
Pallacera vicksburgensis (Conrad, 1848) V
Solenosteira suwanneensis Petuch, n.sp. S
Melongenidae
Myristica crassicornuta (Conrad, 1848) V
Turbinellidae
Clavolithes vicksburgensis (Conrad, 1848) V
Turbinella suwanneensis (Mansfield, 1937) S
Vasum suwanneensis Petuch, n.sp. S
Volutidae
Falsilyria kendrewi Petuch, n.sp. S
Falsilyria mansfieldi (Dall, 1916) F
Volutomitridae
Conomitra crenulata Dockery, 1984 V
Conomitra kendrewi Petuch, n.sp. S
Conomitra staminea (Conrad, 1848) V
Mitridae (Pleioptygmatidae?)
Fusimitra conquista (Conrad, 1848) V
Olividae
Oliva (Omogymna) brooksvillensis (Mansfield, 1937) S
Olivella liscoakensis Mansfield, 1937 S
Olivella vicksburgensis Dockery 1984 V
Marginellidae
Dentimargo dalli Petuch, n.sp. S
Hyalina silicifluvia (Dall, 1916) F
Persicula dockeryi Petuch, n.sp. S
Persicula macneili Petuch, n.sp. S
Persicula suwanneensis Petuch, n.sp. S
Prunum cricae Petuch, n.sp. S
Prunum jessicae Petuch, n.sp. S
Prunum sandrae Petuch, n.sp. (V) S
Conidae
Conus (Leptoconus) cookei Dall, 1916 F

Conus (Asprella) kendrewi Petuch, n.sp. S
Terebridae
Terebra (Terebrellina) divisura Conrad, 1848 V
Turridae
Conorbis porcellanus (Conrad, 1848) V
Crassispirella lyopleura (MacNeil, 1984) V
Euclathurella liveoakensis Mansfield, 1937 S
Pleurofusia brooksvillensis (Mansfield, 1937) S
Pleurofusia dowlingi Petuch, n.sp. S
Pleurofusia plutonica (Casey, 1903) V
Pleurofusia servata (Conrad, 1848) V
Polystira subsimilis (Casey, 1937) V
Cylichnidae
Suwanneascapha lindae Petuch, n.sp. S

APPENDIX 2

Additional Suwannee Formation Gastropods That Were Reported By Mansfield (1937) and E. Vokes (1992) But Were Not Collected (In This Study) At The Terramar Pit. V = Widespread Vicksburgian Species; F = Species Also Known From The Flint River Formation; S = Species Known Only From The Suwannee Formation.

Fissurellidae
"*Diodora chipolana* (Dall)" (probably = *D. mississippiensis* (Conrad, 1848)) V
Cerithiidae
Cerithium georgianum Lyell and Sowerby, 1845 F
"*Cerithium suwanneensis*" Mansfield, 1937
Turritellidae
"*Turritella* cf. *halensis* Dall" (= *Apicula* cf. *halensis*) F
Xenophoridae
"*Xenophora conchyliophora* Born" (= *X. humilis* (Conrad, 1848))
Terebellidae
Terebellum hernandoensis Mansfield, 1937 S
Cassidae
"*Cassis* sp." (= *C. flintensis* Mansfield, 1940) F
Muricidae
Takia portelli (E. Vokes, 1992) S
Buccinidae (?)
"*Latirus* sp." (appears to be a *Cantharus* sp.) S
Volutidae
Lyria mississippiensis Conrad, 1848 V

INSTRUCTIONS TO AUTHORS

THE NAUTILUS publishes papers on all aspects of the biology and systematics of mollusks. Manuscripts describing original, unpublished research as well as review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of meetings and other items of interest to malacologists will appear in a news and notices section.

Manuscripts: Each original manuscript and accompanying illustrations should be submitted in triplicate. Text must be typed on one side of 8½ × 11 inch white paper, double spaced throughout (including literature cited, tables and figure captions), with at least 1 inch of margin on all sides. All pages must be numbered consecutively. If printed on a word processor, the right margin should be ragged rather than justified. Authors should follow the recommendations of the *Council of Biology Editors Style Manual*, which is available from the Council of Biology Editors, Inc., 9650 Rockville Pike, Bethesda, MD 20814, U.S.A. The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latin names and words to be printed in italics must be underlined; leave other indications to the editor. Metric and Celsius units are to be used.

The sequence of sections should be: title page, abstract page, introduction, materials and methods, results, discussion, acknowledgments, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). The abstract page should contain the title and abstract, which should summarize in 250 words or less the scope, main results and conclusions of the paper. The abstract may be followed by a maximum of 8 key words. All references cited in the text must appear in the literature cited section and vice versa. In the literature cited section, all authors must be fully identified and listed alphabetically. Follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included in the pagination. Tables must be numbered and each placed on a separate sheet. A brief legend must accompany each table. Captions for each group of illustrations should be typed on a separate sheet and include a key to all lettered labeling appearing in that group of illustrations.

All line drawings must be in black, high quality ink, clearly detailed and completely labeled. Photographs must be on glossy, high contrast paper. All figures are to be consecutively numbered (figs. 1, 2, 3, ... NOT figs. 1a, 1b, 1c, . . . NOR plate 1, fig. 1 . . .). Illustrations must be arranged in proportions that will conform with the width of a page (6¾ inches or 171 mm) or a column (3¼ inches or 82 mm). The maximum size of a printed figure is 6¾ by 9 inches or 171 by 228 mm. All illustrations must be fully cropped, mounted on a firm, white backing, numbered, labeled and camera ready. The author's name, paper title and figure number(s) should appear on the back. Original illustrations must be between one and two times the desired final size. It is the author's responsibility that the line weight and lettering are appropriate for the desired reduction. Original illustrations will be returned to the author if requested. Color illustrations can be included at extra cost to the author.

Voucher Material: Deposition of type material in a recognized public museum is a requirement for publication of papers in which new species are described. Deposition of representative voucher specimens in such institutions is strongly encouraged for all other types of research papers.

Processing of Manuscripts: Upon receipt, every manuscript is acknowledged and sent for critical review by at least two referees. These reviews serve as the basis for acceptance or rejection. Accepted manuscripts are returned to the author for consideration of the reviewers' comments. A finalized version of the manuscript is returned to the editor and sent to press. Two sets of proofs are sent to the author for correction. Changes other than typesetting errors will be charged to the author at cost. One set of corrected proofs should be sent to the editor as soon as possible. Authors with institutional, grant or other research support will be billed for page charges at the rate of $60.00 per printed page.

An order form for reprints will accompany the proofs. Reprints may be ordered through the editor.

Manuscripts, corrected proofs and correspondence regarding editorial matters should be sent to: Dr. M.G. Harasewych, Editor, Division of Mollusks, NHB stop 118, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, U.S.A.

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